Cranial anatomy and diversity of the Norian phytosaurs of Southwestern Germany

Volume 1

Text

by

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Abstract

Phytosaurs are the most basal group of crurotarsan archosaurs. Superficially resembling crocodiles in habit and probably also in their ecological requirements, they form an important component of terrestrial vertebrate communities in the Late Triassic.

The phytosaurs from the Stubensandstein deposits (Norian) of southwestern Germany are among the first representatives to become known of the group. However, our poor knowledge of European Norian phytosaurs is well exemplified by many morphological details of the cranium that in the course of this study were found to be hitherto unknown, or to be at variance with the literature. Virtually all phytosaur specimens from these deposits were examined to established their taxonomic status. The specimens comprise four valid species, which are referred to the genera *Nicrosaurus* FRAAS, 1866 and *Mystriosuchus* FRAAS, 1896. Both genera and all species are redefined on the basis of shared derived characters. The aim of this thesis is to redescribe the cranial anatomy of each taxon, a prerequisite to determine the variability and to test the validity of cranial characters that have been utilised to establish phylogenetic relationships among phytosaurs.

A comprehensive skull osteology and a study of the variation in cranial characters of *Nicrosaurus kapffi* (MEYER, 1860) forms the main part of the thesis. The complete upper dentition is described in order to determine the positional variation of dental characters. *Nicrosaurus kapffi* is characterised by two features of its prenarial crest. Two morphs are recognised among the specimens based mainly on different skull width. The distinction is congruent with the distribution of other dimorphic features of the postorbital part of the skull and details of the crested rostrum, many of which are currently employed in phytosaur taxonomy. The intraspecific variation is interpreted as sexual dimorphism. The study demonstrates also that other characters are actually variable at species level and can provide only limited taxonomic and phylogenetic information. These include, most importantly, a reduction of the suborbital opening, a partly persisting parietal foramen, and, varying individually, the configuration of a number of dermal skull bones.

The slender-snouted and gracile specimens previously referred to *Belodon plieningeri* MEYER, 1844 actually represent a species of *Nicrosaurus*, here referred to as *Nicrosaurus* species B. A hitherto undescribed skull provides important missing information on the temporal region in this taxon. *Nicrosaurus* species B is more derived than *Nicrosaurus kapffi* in having, among more uncertain characters, a more elongated squamosal with a pointed squamosal tip and a narrower supratemporal fenestra. *Nicrosaurus* species B shows the same two intraspecific morphotypes regarding skull width, but, additionally, a significant variation of the shorter prenarial crest can be observed.

Additional cranial data is provided to characterise the highly derived *Mystriosuchus planirostris* (MEYER, 1863), the type species of the genus. Previous suggestions that a particular skull represents a different species of *Mystriosuchus* are confirmed. The occipital aspect of this skull is redescribed, and a new reconstruction of the braincase is presented. The hitherto unnamed species is distinguished by numerous cranial characters, including details of the temporal region, an orbitosphenoid, a supernumerary bone in the occipital region, and possibly a premaxillary crest.

A phylogenetic analysis of 22 phytosaur taxa based on 49 characters using PAUP was conducted. As a preliminary result, the Paleorhininae were found not to be monophyletic as previously suggested, but to represent the paraphyletic stem-group of all other phytosaurs (Phytosauridae). Secondly, *Mystriosuchus* is not closely related to any non-phytosaurid phytosaur, but the most derived Phytosauridae forming a clade with *Pseudopalatus pristinus* and *Arribasuchus buceros*.

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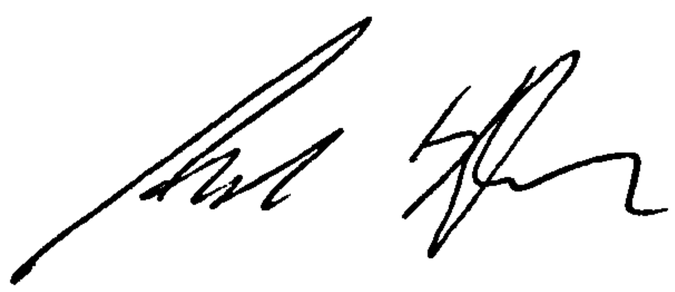
Declaration

The work of this thesis is the result of independent research, except where acknowledgement is made in the text. It has not been submitted to any other university for any other qualification.



Axel Hungerbühler, May 1998

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Chapter 1

Introduction

Phytosaurs, which are often also referred to as parasuchians, form a well-defined clade firmly embedded in the Crurotarsi (GOWER & WILKINSON 1996), the line of archosaurian reptiles that leads to modern crocodiles. Phytosaurs are entirely restricted to the Late Triassic, a time span of roughly 25 million years, and are represented in many terrestrial deposits in North America, Europe, North Africa, and India. Superficially, phytosaurs resemble crocodiles because of their almost identical skull shape and body form, and phytosaurs like their most modern counterparts the crocodiles were probably the dominate semiaquatic freshwater predator of their time. The first phytosaurs appear in the Carnian (with the potential exception of *Mesorhinosuchus*, reportedly derived from early Triassic strata), and by the end of that stage and throughout the Norian, phytosaur remains are the most abundant vertebrate fossils found in almost all fluvial deposits of this age in the northern hemisphere. After a short evolutionary history spanning only about 25 Ma, the group apparently became extinct at the end of the Triassic. There is no safe record of a phytosaur beyond the Triassic/Jurassic boundary (BUFFETAUT 1993).

Section 1.1
The fossil record of phytosaurs in Europe

The fossil record of phytosaurs in Europe is remarkably complete, ranging from the Upper Carnian to the very end of the Triassic, and is only surpassed by North American phytosaur assemblages in terms of the temporal range and abundance of material. As an introduction, the taxa may be conveniently subdivided into four groups according to their stratigraphical distribution. I will only deal with those taxa that are represented by enough substantially complete cranial material to be considered valid taxa, or that, pending investigation, are potentially valid taxa. Table 1.1 provides a comprehensive list and the details of all European phytosaur taxa that have been established so far, and also lists

Table 1.1 The fossil record of phytosaurs in Europe. Taxa are listed according to stratigraphic occurence

taxon	material	locality or spatial distribution	stratigraphical derivation and age	main anatomical reference	comments
Mesorhinosuchus fraasi (JAEKEL, 1910)	partial skull	(?) Bernburg (Thuringia: Fig. 1.1A)	(?) middle Buntsandstein; Scythian	JAEKEL (1910)	non-phytosaurid phytosaur; holotype and only specimen lost
Francosuchus broilii KUHN, 1932	skull lacking posterior face and part of the rostrum	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1932, 1936)	type species
Francosuchus latus KUHN, 1932	skull lacking the rostrum	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1932)	—
Francosuchus angustifrons KUHN, 1936	skull lacking the rostrum	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1936)	—
Ebrachosuchus neukami KUHN, 1936	complete skull	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1936)	—
Mystriosuchus cf. *plieningeri*	fragmentary cast of a skull; fragmentary right mandibular ramus	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1932, 1936)	indeterminable phytosaur
Mystriosuchus sp.	right mandibular ramus	Ebrach (Franconia, Bavaria: Fig. 1.1A)	Blasensandstein (equivalent of Kieselsandstein); Carnian	KUHN (1932)	indeterminable phytosaur
cf. *Francosuchus trauthi* HUENE, 1939	snout fragment	Lunz (Austria)	lower parts of Opponitzer Beds, Late Carnian	HUENE (1939)	non-phytosaurid phytosaur
Phytosaurus cylindricodon JAEGER, 1828 (= *Phytosaurus cubicodon* JAEGER, 1828)	natural mould of a fragmented mandible	Rübgarten (Württemberg: Fig. 1.1A)	middle Stubensandstein; Norian	JAEGER (1828); HUENE (1911); this study	*nomen dubium* (see chapter 4)
Belodon plieningeri (MEYER, 1844)	1 isolated tooth, 1 mandible fragment	Löwenstein (Württemberg: Fig. 1.1A)	Stubensandstein, unspecified; Norian	MEYER in MEYER & PLIENINGER (1844); MEYER (1847-55); this study	*nomen dubium* (see chapter 4); syntypes lost
Nicrosaurus kapffi (MEYER, 1860)	see section 2.2	see section 2.2	middle (and perhaps lower) Stubensandstein; Norian	MEYER (1863); this study	—
Nicrosaurus sp. nov. [see HUNT 1994]	see section 2.3	see section 2.3	middle (and perhaps lower) Stubensandstein; Norian	MEYER (1861, 1865b); this study	substitute name for *Belodon plieningeri* sensu MEYER (1861); *Nicrosaurus* species B of this paper
Mystriosuchus planirostris (MEYER, 1863)	see section 3.2	see section 3.2	middle Stubensandstein, Dachsteinkalk; Calcare di Zorzino; Norian	MCGREGOR (1906); this study	—
Mystriosuchus sp. nov. [see HUNT & LUCAS 1989b; LONG & MURRY 1995]	see section 3.3	see section 3.3	middle Stubensandstein; Norian	HUENE (1911); this study	*Mystriosuchus* species B of this paper

Table 1.1 (continued)

taxon (as named by first author)	material	locality or spatial distribution	stratigraphical derivation and age	main anatomical reference	comments
Coburgosuchus goeckeli HELLER, 1954	skull lacking the rostrum and the mandible	Coburg (Franconia, Bavaria: Fig. 1.1A)	upper Burgsandstein (equivalent of upper Stubensandstein)	HELLER (1954)	—
Rileyasuchus bristolensis (HUENE, 1902) (= *Rileya stutchburi* HUENE, 1920)	humerus, two vertebral centra (syntypes)	Durdham Down, Bristol (Avon, England, UK)	fissure fillings, (?) Norian	HUENE (1902, 1908, 1914)	indeterminable archosaur; vertebrae referred to prosauropod (HUENE 1914)
Paleosaurus platyodon (RILEY & STUTCHBURY, 1840)	one isolated tooth; another tooth and isolated postcranial elements referred	Durdham Down, Bristol (Avon, England, UK)	fissure fillings, (?) Norian	RILEY & STUCHBURY (1840); HUENE (1908)	holotype tooth belongs to an indeterminable heterodont phytosaur (pers. obs.)
Angistorhinopsis ruetimeyeri (HUENE, 1911)	basicranium, teeth, vertebrae, 2 ilia, 2 femora and 4 osteoderms (isolated specimens, syntypes)	Niederschönthal near Basel (Switzerland)	Knollenmergel; Upper Norian	HUENE (1911)	indeterminable Phytosauria
	teeth, pterygoid, palatine, postcrania (isolated specimens)	Quarry BAERECKE, Halberstadt, (Sachsen-Anhalt: Fig. 1.1A)	Rhaetic	HUENE (1922)	indeterminable phytosaur specimens
	partial skull, postcrania of presumably one individual	Steinlah near Salzgitter (Niedersachsen: Fig. 1.1A)	Rhaetic	HUENE (1922)	potentially valid taxon more derived than *Nicrosaurus*
Rutiodon ruetimeyeri (HUENE, 1911), or alternatively referred to an indeterminable phytosaur	isolated teeth	Saint-Nicholas-de-Port, Provenchère-sur-Meuse (both France); Medernach (Luxembourg)	Norian and Rhaetic bonebeds	BUFFETAUT & WOUTERS (1986); CUNY (1995); CUNY & RAMBOUER (1991); CUNY *et al.* (1995); GODEFROIT & CUNY (1997)	teeth of indeterminable, strongly heterodont phytosaur
Mystriosuchus sp.	teeth, squamosal, mandibular fragments, postcrania (all isolated specimens)	Quarry BAERECKE, Halberstadt, Sachsen-Anhalt	Rhaetic	HUENE (1922)	indeterminable Phytosauridae, non *Mystriosuchus*
Palaeosaurus stricklandi DAVIS, 1881	isolated tooth	Coombe Hill, Cheltenham (Gloucestershire, England, UK)	Rhaetic	DAVIS (1881)	tooth of an indeterminable phytosaur
teeth comparable to *Angistorhinopsis*	3 isolated teeth	Hettange Grande (Lorrain, France)	Upper Hettangian (stratotype section)	HUENE & MAUBEUGE (1954)	indeterminable heterodont phytosaurs; most likely reworked from older deposits

Table 1.1 (continued)

taxon (as named by first author)	material	locality or spatial distribution	stratigraphical derivation and age	main anatomical reference	comments
Misidentified or dubious phytosaur specimens					
Parasuchia (includes specimens of *Cladeiodon lloydi* OWEN, 1841)	isolated teeth; ilium fragment	Leamington, Warwick, Bromsgrove (Warwickshire, England, UK)	Bromsgrove Sandstone Formation; Anisian	GALTON & WALKER (1996: figs. 2C, 3D-T, 4A-F)	phytosaurian nature impossible to assess based on data presented and fthe igures given; in parts probably rauisuchian (BENTON & GOWER 1996)
Parasuchia	humerus	Blindlach near Bayreuth (Bavaria)	Upper Muschelkalk ; Anisian/ Ladinian	HUENE (1920)	referred to the prolacertiform *Tanystropheus conspicuus* (WILD 1973)
Parasuchia	radius	Wesseln (Niedersachsen)	Upper Muschelkalk; Anisian/ Ladinian	HUENE (1958)	indeterminable
Zanclodon arenaceus E. FRAAS, 1896	symphyseal part of a mandible	Feuerbach near Stuttgart (Württemberg: Fig. 1.1A)	Schilfsandstein; Carnian	HUENE (1902)	indeterminable long-snouted archosaur
Termatosaurus albertii PLIENINGER, 1844	various isolated teeth (syntypes)	Täbingen (Württemberg) and other Württemberg localities	Rhaetic bonebeds	PLIENINGER in MEYER & PLIENINGER (1844)	*nomen dubium*; doubtfully phytosaurian

unnamed specimens or invalid taxa, which nevertheless may be important for determining the spatial distribution and stratigraphical record of phytosaurs in Europe. A number of misidentified specimens, and taxa usually included in Phytosauria, but that are actually of uncertain affinities, are listed at the end of the table.

1.1.1 Carnian phytosaurs

KUHN (1932, 1936) described in detail the cranial anatomy of four nominal taxa (*Francosuchus broilii*, *Francosuchus latus*, *Francosuchus angustifrons*, and *Ebrachosuchus neukami*), each represented by one individual, and referred mandibular material to two unnamed species of *Mystriosuchus*. All specimens are derived from a single quarry in the Blasensandstein near Ebrach in Franconia (Fig. 1.1A), which is contemporaneous with the Kieselsandstein of Southwest Germany (Fig. 1.2A). *Francosuchus* and *Ebrachosuchus* clearly belong to the most primitive phytosaurs known, as indicated by numerous characters such as the far anteriorly placed external nasal openings or the primitive state of the supratemporal fenestrae. Recently, HUNT & LUCAS (1991) and LONG & MURRY (1995) synonymised KUHN's genera with the North American primitive phytosaur *Paleorhinus*, and tentatively recognised only one species, *Paleorhinus neukami*. A full alpha-taxonomical revision of the Ebrach phytosaurs has still to be undertaken, however. *Francosuchus* and *Ebrachosuchus*, among them some of the best preserved examples of a primitive phytosaur, might serve as the starting point for a long overdue revision of the most primitive (i.e. non-phytosaurid) phytosaur genera, which include also *Paleorhinus*, "*Parasuchus*", *Promystriosuchus*, and *Arganasuchus*.

1.1.2 Lower and Middle Norian phytosaurs

The Stubensandstein of Württemberg has yielded the majority of phytosaur specimens from Europe. Currently, four taxa are recognised, and all are much more advanced than the Ebrach phytosaurs. *Nicrosaurus kapffi* is a robust phytosaur, characterised by a peculiar bony crest on the top of the snout (MEYER 1863). A second, more gracile form, commonly known as *Belodon plieningeri*, shows many similarities to *Nicrosaurus kapffi*, but has been only poorly described so far (MEYER 1865b). *Mystriosuchus* represents one of the most derived phytosaurs known. The genus is represented by numerous skulls and even articulated partial postcrania of the type species *Mystriosuchus planirostris*, a form well adapted to a piscivorous life-style judging by its strongly elongated snout and the nature of the dentition (MCGREGOR 1906). It has also been reported from Austria and Italy. A single, larger, more robust skull has been

identified as a second, unnamed species of *Mystriosuchus* (HUNT & LUCAS 1989b; LONG & MURRY 1995).

1.1.3 Upper Norian phytosaurs

HELLER (1954) described and named *Coburgosuchus goeckeli* on the basis of an incomplete, but otherwise well preserved skull derived from the upper Burgsandstein of Coburg in Franconia (Fig. 1.1A). The upper Burgsandstein is the Bavarian equivalent of the upper Stubensandstein, and *Coburgosuchus* is thus younger than any Stubensandstein phytosaur from Württemberg (Fig. 1.2A), representing the only substantial phytosaur find from the European Upper Norian. It was realised long ago that *Coburgosuchus* shows close affinities with *Nicrosaurus kapffi* (GREGORY 1969; WESTPHAL 1976), or may represent a subjective junior synonym of *Nicrosaurus* (HUENE 1956; KUHN 1961a, b). However, the synonymy cannot be established as long as the hypodigm of the genus *Nicrosaurus* is not explicitly defined, and close comparisons between both genera, including a redescription of the type of *Coburgosuchus*, have been made.

1.1.4 Rhaetian (or Rhaetic) phytosaurs

Angistorhinopsis ruetimeyeri (*Rutiodon ruetimeyeri* in GREGORY 1962a and WESTPHAL 1976) is currently the only accepted phytosaur species from the uppermost Triassic (Rhaetian) of Europe. However, the taxon, originally based on an undiagnostic basicranium from beds in Switzerland equivalent to the Knollenmergel (HUENE 1911), is most probably invalid. The only specimen from the uppermost Triassic sufficiently well preserved to potentially represent a valid taxon is a partial skull with associated postcranial elements from the Rhaetic bonebed near Salzgitter (Fig.1.1A; Fig. 1.2). It was described by HUENE (1922), and subsequently regarded as the hypodigm of *Angistorhinopsis ruetimeyeri*. According to the description, the specimen is more derived than *Nicrosaurus* in having a rounded parietal-supraoccipital complex like *Mystriosuchus* (HUENE 1922: fig. 114a), but differs strikingly from *Mystriosuchus* in showing a thin postorbito-squamosal bar with extended medial lamella (HUENE 1922: fig. 114h). It should be noted that HUENE's (1922) frequently copied figures 128-130 of the entire skull of *Angistorhinopsis* are largely reconstructed, and in parts based on phytosaurian skull bones from other Rhaetian localities. The Salzgitter skull needs to be re-examined and, in particular, more detailed comparisons with other highly derived phytosaur taxa such as *Pseudopalatus* are necessary to establish its taxonomic status.

1.1.5 Conclusions

Although it is obvious from this short overview, that much needs to be done to improve our knowledge of European phytosaurs, the material dealt with in this study was limited chronologically and geographically to forms from the Stubensandstein of Southwest Germany. The Stubensandstein has yielded the best fossil record of phytosaurs in Europe, both in terms of number of specimens and completeness of preservation. Furthermore, the Stubensandstein forms include the "classical" finds of phytosaurs often referred to in the literature. However, these taxa are clearly in need of revision (BALLEW 1989; LONG & MURRY 1995), and their anatomy has never been fully described nor dealt with comprehensively. This work will provide not only a basis for comparisons with the much better known American and North African phytosaurs, but also the necessary materials for reassessing the status and phylogenetic position of less well known taxa including *Coburgosuchus* and *Angistorhinopsis*.

Section 1.2
Geological setting

1.2.1 Stratigraphy

With a few exceptions from the marine Alpine Triassic, the phytosaur taxa from Europe are exclusively derived from the Upper Triassic Keuper succession. This section aims to give an introduction to the deposits and depositional environments of the Keuper and to provide a geological and stratigraphical framework of the Stubensandstein. A synthesis of the Keuper succession in central Europe is compiled in Figure 1.2A, largely based on the deposits in South Germany. The lithologic description follows GEYER & GWINNER (1991) and AIGNER & BACHMANN (1992), and I refer to these publications for more detailed references.

The Lower Keuper or Lettenkeuper starts with the Grenz-bonebed which unconformably overlies the marine Muschelkalk deposits of the Middle Triassic. The Lettenkeuper is mainly a succession of variegated shales intercalated with thin dolomitic beds, probably laid down in a brackish-water environment. Several fluvial sandstone beds occur regionally in different stratigraphic positions within the succession, the most important being the Lettenkeuper-Hauptsandstein.

A gradual shift towards a marine depositional environment resulted in the deposition of the first member of the Middle Keuper, the Gipskeuper, which includes stacked dolomite-gypsum sequences topped by deposits in a playa-like environment. The Schilfsandstein was deposited throughout the German Basin following an erosional phase on the former playa plain. The unit comprises a thin-bedded mudrock facies ("Normalfazies") and a sandstone facies ("Flutfazies") derived from the Fennoscandian High to the far Northeast. The Schilfsandstein probably represents the deposits of an incised fluvial drainage system rather than a deltaic sandstone as interpreted previously (WURSTER 1964). Coloured mudstones with gypsum deposited in an arid desert-like environment make up the Rote Wand. The Kieselsandstein comprises a mudrock facies similar to the Rote Wand (Bunte Mergel) and, interdigitating with the mudrocks, two sandstone beds of fluvial origin, the Kieselsandstein proper. The Kieselsandstein also includes a series of lacustrine dolomitic beds, the Lehrbergschichten. The overlying Stubensandstein includes four thick fluvial sandstone units. These are treated in more detail below. The Stubensandstein succession is followed by the Knollenmergel Beds, a unit consisting of uniform, unstratified mudrocks of regionally variable thickness (10-50 m), which are characterised by dispersed carbonate concretions.

In northern and eastern Germany, the Knollenmergel is topped by extensive Upper Keuper beds, the basal unit being thick fluvial sandstones ("Hauptsandstein") that grade into fine-grained floodplain deposits. Both facies are for convenience referred to the Lower Rhaetian. These again are overlain unconformably by marine sandstones and shales, which can be safely dated as Rhaetian based on a fauna including the bivalve *Rhaetavicula contorta*. In South Germany, the Upper Keuper comprises only one member, which is known as the Rhät. The Rhät is only preserved in patches and represents the much condensed deposits of a coastal delta environment, the result of extensive reworking during the marine Rhaetic transgression. These deposits include the "Rhät-sandstone", which contains the well-known Rhaetic bonebeds, and the much thinner "Rhät-shales".

In the Late Triassic, the Southwest of Germany formed a sub-basin of the Germanic Keuper Basin (Fig. 1.1C). In its centre, fine-grained siliciclastic sediments intercalated with allochthonous dolomitic beds and evaporites, the so-called Steinmergel-Keuper, slowly accumulated in a playa-like environment. Extensive alluvial fans protruded repeatedly into the sub-basin from the Bohemian Massif and Vindelician High to the east and southeast. This resulted in more complex series of marginal basin deposits (Sandstein-Keuper, which includes Kieselsandstein and Stubensandstein). Both units consist in general of multistoried fluvial sandstones interbedded with siltstones, claystones, and pedogenetic calcretes. The upper part of the marginal deposits, the

Stubensandstein, is defined by a succession of four heterochronous sandstone units (termed 1st - 4th Stubensandstein) which show a maximum total thickness of 140 m near the former high-land, but gradually diminish in thickness and pinch out toward the centre of the subbasin (Fig. 1.2A). The sandstone units, as shown in Figure 1.2B, include a variety of fluvial architectural elements that indicate deposition in channels, by sheet floods, and crevasse splays, but also more fine-grained sediments deposited on floodplains and in backswamps (e.g. JUNGHANS 1997). The 1st to 4th Stubensandstein are separated by thick mudrocks, which show evidence of pedogenetic processes (caliche, root horizons) and probably slowly accumulated in a floodplain or playa environment.

Lithostratigraphically, the marginal deposits are further subdivided into the lower, middle and upper Stubensandstein on the basis of a few isochronous horizons (calcareous conglomerates, i.e. reworked caliche beds, dolomitic limestone beds, and the erosional base of the 2nd Stubensandstein). The calcareous horizons can be correlated with marine-influenced dolomitic layers in the basin centre (BRENNER & VILLINGER 1981). Note that these lithostratigraphic units include also fine-grained deposits (Basisletten, Hangendletten, Zwischenletten in Figure 1.2B), and have been interpreted "quasi-isochronous" (BRENNER 1973) in contrast to the alluvial fans of the 1st to 4th Stubensandstein (Fig. 1.2B). STOLL (1929) and subsequent workers presented a more detailed division of the middle Stubensandstein in central and western Württemberg, identifying three distinguishable but presumably heterochronous sandstone units within the 2nd Stubensandstein, for which the acronyms "sc1", "sc2", and "sc3" have been established. Because of the palaeogeographical situation, the facies units sc1 to sc3 gradually taper and interdigitate with the fine-grained sediments of the central basin towards the west and southwest. At the transition of marginal and central basin deposits, the younger Knollenmergel represents, at least in parts, a heterochronous facies unit deposited probably in a playa environment: in southern Württemberg, the lower beds of the Knollenmergel replace the third and fourth Stubensandstein, which were laid down contemporaneously in central and eastern Württemberg (BRENNER & VILLINGER 1981).

1.2.2 The age of the Stubensandstein deposits

Two alternative hypotheses have been advocated to calibrate the lithostratigraphic units of the German Keuper Succession (reviewed in BENTON 1994a, b). Both views unanimously agree that the Stubensandstein must be considered Norian in age, but conflicting palynologic, magnetostratigraphic and palaeoclimatic evidence has led to different assessments of the time span of this unit within the stage. Interpretation (A) suggests that the Stubensandstein is restricted in time to the middle and upper part of the

Norian. According to the alternative view (B), the Stubensandstein comprises almost the whole Norian, with the exception of the Knollenmergel, which is commonly referred to the uppermost part of the Norian.

There have been various attempts based on the vertebrate faunal content to correlate the Stubensandstein deposits either with the marine Triassic strata in the Alpine region, or with other terrestrial Late Triassic deposits. WILD (1989) assigned a Middle Norian age to the lower Stubensandstein because of the occurrence therein of *Aetosaurus* and in the datable Calcare di Zorzino in North Italy. This points towards a Middle to Late Norian Age for the whole Stubensandstein deposits, lending further support to interpretation (A). LUCAS & HUNT (1993) proposed the Revueltian landvertebrate faunachron for the southwestern United States (Chinle Formation) and suggested an Early Norian age. The Revueltian is characterised, among other vertebrates, by the aetosaur *Paratypothorax* (see also HUNT & LUCAS 1992), which occurs in the lower Stubensandstein (WILD 1991), but is definitely present in the middle Stubensandstein of Kayh (HUNGERBÜHLER, unpublished data). This argues, by contrast to WILD's hypothesis, for an Early Norian age for both subunits, and is broadly consistent with interpretation (B).

Both biostratigraphical hypotheses may be tested when exact dates are established for specimens referable to the phytosaur *Mystriosuchus* from the marine Dachsteinkalk of the Austrian Alps (reported briefly by BUFFETAUT 1994). A preliminary note by RENESTO & PAGANONI (1998) on a specimen of *Mystriosuchus planirostris* from Endenna (North Italy) supports a Middle Norian age for that species. In the German Basin, *Mystriosuchus* is so far restricted to the middle Stubensandstein (Appendix C).

Several fundamental problems plague all stratigraphical correlations that utilise vertebrate remains as index fossils of the Keuper. Firstly, the exact derivation of a good number of vertebrate fossils is unknown, and *in retrospect*-referals (especially of most individuals found in the last century, such as all *Nicrosaurus* from the Stuttgart region) remain questionable. For example, the referal of the *Aetosaurus* specimens from Kaltental to the lower Stubensandstein by WILD (1989) is debatable, since the Kaltental quarry could well have been operating in the middle Stubensandstein (e.g. BRENNER 1973; see discussion in Appendix C). Secondly, the limited number of finds renders it difficult to establish the exact stratigraphical range of a given taxon. This is most obvious in the case of taxa essentually known from one particular locality (e.g. *Aetosaurus* at Kaltental). Furthermore, despite broadly similar depositional and environmental settings, not a single identifiable vertebrate specimen has ever been found in the sandstones of the upper Stubensandstein. This means that our knowledge of the stratigraphical range of all Stubensandstein vertebrates is restricted *a priori* to the lower and middle Stubensandstein. Another factor not accounted for in previous attempts of dating is the restricted occurrence of taxa (spatially or stratigraphically) because of habitual or

palaeoenvironmental requirements (e.g. *Mystriosuchus*). Thirdly, the significance of vertebrate biochrons for correlating stratigraphic units both on a regional and especially on a transcontinental scale has never been subject to a critical reevaluation. The acceptance of a landvertebrate faunachron depends largely on the acceptance of an underlying alpha-taxonomic scheme (e.g. LONG & MURRY 1995; regarding phytosaurs, see subsection 2.3.1). Most importantly, the correlations suggested so far still need to be tested and substantiated by means of dating techniques independent from biostratigraphy.

In summary, contradictory stratigraphical evidence results in two different assessments of the age of the Stubensandstein. Currently, there is no sufficient biostratigraphical data available to correlate in a convincing fashion one of the subunits of the Stubensandstein with the marine standard zones of the Alpine Triassic, and resolve this question. However, I consider the supposition that the Stubensandstein spans most of the Norian as the more likely interpretation for the present.

Section 1.3
The phytosaurs of the Stubensandstein: a historical approach

The former state of Württemberg is the classical region where research on the terrestrial deposits of the Late Triassic and their fossil vertebrates began. Here, the first poorly preserved remains of phytosaurs, *Phytosaurus cylindricodon* and *Phytosaurus cubicodon*, were described (JAEGER 1828), giving rise to the misleading name "plant-eating reptiles" that is widely used to characterise the whole group. In the following decades, more fragmented material accumulated from Löwenstein (northern Württemberg, Fig. 1.1B) and the surroundings of Stuttgart, and a second phytosaur taxon, *Belodon plieningeri*, was named, based on two teeth and jaw remains (MEYER & PLIENINGER 1844; MEYER 1847-55; PLIENINGER 1857). However, the nature of these reptiles remained mysterious. Finally, in the second half of the last century, the first complete skulls became available to science because of the assiduous activities of a private collector, Sixt Friedrich Jacob von KAPFF. Within 15 years, KAPFF collected about half of all phytosaur specimens that are known from Europe today from quarries in the Stubensandstein around Stuttgart (central Württemberg, Fig. 1.1B). These include nearly all known specimens of *Nicrosaurus kapffi*, two skulls usually referred to *Belodon plieningeri*, and numerous isolated postcranial remains (MEYER 1861, 1863, 1865b; HUENE 1913, 1922). Moreover, his activities brought to light a great diversity of

contemporaneous tetrapods, including temnospondyls, early turtles, aetosaurs, a rauisuchian, as well as prosauropod and theropod dinosaurs (BENTON 1993). KAPFF sold his important collection, in several instalments, to the SMNS and BMNH, and with his death in the 1880s, collection of Stubensandstein vertebrates essentially ceased in the Stuttgart area.

Shortly after the turn of the century, several phytosaur skulls were found in a Stubensandstein quarry at Pfaffenhofen in the Stromberg Mountains (northern Württemberg, Fig. 1.1B). Although the most informative skull of "*Belodon plieningeri*", a taxon already described from the Stuttgart area, was included among them, the specimens attracted little interest. The significance of these finds was perhaps underestimated, but, more likely, the phytosaur remains were overshadowed by the abundant dinosaurs that were recovered at the same site (FRAAS 1913, 1914). Another reason might be, that at this time the Stubensandstein deposits in the vicinity of Aixheim in southern Württemberg (Fig. 1.1B) became particularly productive in terms of phytosaur discoveries. The skull fragment of a slender-snouted phytosaur, the type of *Mystriosuchus planirostris*, had already been collected there in the early 1860s, following an increased interest in Keuper fossils after KAPFF's spectacular finds (ESER 1907; MEYER 1863). Between 1896 and 1920, the quarries around Aixheim and Trossingen continued to produce numerous phytosaur skulls and postcrania. The outstanding discoveries were the first articulated partial skeletons of phytosaurs (*Mystriosuchus planirostris*: MCGREGOR 1906; HUENE 1922) and an impressive skull from Trossingen, which actually represents a second species of *Mystriosuchus*. At the time of HUENE's description of the Trossingen skull in 1911, the German forms *Nicrosaurus*, "*Belodon*", and *Mystriosuchus* represented the phytosaur taxa on which almost the whole knowledge of this group was based.

The focus of phytosaur research then shifted to North America, in particular to the Chinle Formation and Dockum Group of the southwestern United States. New taxa were found in rapid succession (e.g. CASE 1922; LEES 1907; MEHL 1915, 1916, 1928) and some of them were described in remarkable detail and accuracy (CASE 1929; CAMP 1930), becoming the main references for phytosaur anatomy. More recently, well preserved specimens became known from India (CHATTERJEE 1978) and Morocco (DUTUIT 1977a, 1977b), which greatly enhanced our understanding of phytosaurs. In Germany, meanwhile, the likelihood of more and more informative finds has rapidly decreased because of the decline of the Stubensandstein quarrying industry during the 1930's and the post-war decades. It is therefore more than ever necessary to reinvestigate existing specimens and to review the basic evidence, in order to update our knowledge of the earliest known members of the group.

Section 1.4
The aims of the study

Although the first phytosaurs were described well in the middle of the last century, and morphological data from representatives of ingroup clades have been largely available since the end of the first half of this century, the taxonomy of phytosaurs is still in a state of flux. Three different taxonomic and nomenclatural schemes have been proposed in the last ten years (BALLEW 1989; HUNT 1994; LONG & MURRY 1995). While focusing mainly on the North American phytosaur taxa, these studies largely excluded the contemporaneous German counterparts, on the grounds that these are too inadequately known - a conclusion already drawn by FRAAS (1896) over a hundred years ago. Indeed, although a number of important descriptive studies on the German phytosaurs have been carried out (MEYER 1861, 1863, 1865b; MCGREGOR 1906; HUENE 1911, 1922), our knowledge of the European forms is still poor. Furthermore, BALLEW (1989) and in parts LONG & MURRY (1995) for the first time defined the operational taxonomic units (morphospecies) by autapomorphies, and a number of new cranial characters were introduced into the literature.

The objectives of the taxonomic part of this study are:

(1) to provide additional morphological data on the Norian phytosaurs from southwestern Germany. This information has been available for a long time but has not been considered so far. One of the reasons for this is that previous studies made little use of the abundant material, but focused on single individuals, either the first specimen that became known, or specimens thought to be representative of a particular taxon. This study tries to overcome these shortcomings by studying all the material referable to each phytosaur taxon.

(2) to find new, and to test previously suggested, shared derived characters that define the Stubensandstein phytosaur species and higher categories (genera). This forms the basis for a systematic review of the taxa involved.

(3) to test the intraspecific stability of character states that have been suggested to be taxonomically (and phylogenetically) significant by studying character state variation within a monophyletic phytosaur species.

The phylogeny of phytosaurs has always been controversial. In the last decade, two hypotheses have been proposed (BALLEW 1989; LONG & MURRY 1995), the first of them based on a cladistic analysis. These phylogenetic schemes differ essentially in one

point only: whether the genus *Mystriosuchus* has to be placed in a sistergroup-relationship to a basal clade comprising the most primitive phytosaurs (Paleorhininae *sensu* LONG & MURRY 1995) or whether the genus represents the most derived clade of phytosaurs, closely related, to or even congeneric with *Pseudopalatus* (BALLEW 1989). While this seems to be a minor issue at first glance, it has substantial bearing on our understanding of the evolution of character traits within phytosaurs. The contradictory opinions are rooted in the incongruent distribution of character states in *Mystriosuchus*, which shows a mixture of primitive features (most notably the lack of a posterior process of the squamosal) and highly advanced features (among others, a greatly depressed parieto-squamosal bar). Depending on the preferred hypothesis, a different set of characters must have evolved convergently within Phytosauria. A decision based on functional considerations or any sort of weighting of characters seems inappropriate, since both sets include characters whose functional context are essentially unknown. Moreover, the "weight" of some features cannot be assessed because they are unique to phytosaurs among archosaurs. The phylogenetic relationships of *Mystriosuchus* are reinvestigated here using cladistic methods, and the most parsimonious hypothesis is used to determine which character states represent phylogenetic synapomorphies and which must have arisen independently or reversed in at least one other group.

Section 1.5
The structure of the thesis

The following chapter deals with the cranial anatomy and systematics of the genus *Nicrosaurus*. In section 2.1, *Nicrosaurus* is redefined based on characters unique among phytosaurs. The occurrence of *Nicrosaurus* outside of Europe, which has been postulated previously, is discussed and rejected.

In section 2.2, a comprehensive osteology of the type species *Nicrosaurus kapffi* is presented. This includes a detailed description of the dentition focusing on the positional variation in this species, and some dental characters are tentatively suggested which can be useful in phytosaur taxonomy. *Nicrosaurus kapffi* is defined by shared derived characters. This is followed by a study of the variation of cranial characters at intraspecific level. The varying characters are referred to individual, ontogenetic, and sexual variation, which leads to conclusions about the utility of these characters in phytosaur taxonomy and phylogeny.

The third part of the chapter, section 2.3, deals with the specimen known under the binomen "*Belodon plieningeri*". New morphological data for "*Belodon plieningeri*" is presented, focusing on the previously neglected, but most informative, specimen SMNS 12593. The characters found in the assemblage are compared with those of *Nicrosaurus kapffi* and the American species *Pseudopalatus pristinus*, and it is concluded that "*Belodon plieningeri*" represents a species of *Nicrosaurus* that has still to be formally named. In this study, it will be referred to as *Nicrosaurus* species B. The non-diagnostic characters distinguishing *Nicrosaurus kapffi* from *Nicrosaurus* species B are listed and their significance discussed.

The anatomy and taxonomy of the genus *Mystriosuchus* is the subject of chapter 3. Following the first identification of two species by HUNT & LUCAS (1991a), the generic definition of *Mystriosuchus* is briefly reviewed and emended in section 3.1. Section 3.2 presents additional information on the skull of the type species, *Mystriosuchus planirostris*, and determines the unique derived characters of this species. In section 3.3, the cranial anatomy of a new species, which is tentatively named *Mystriosuchus* species B, is described in more detail in comparison to the original description of both the only known specimens. A number of peculiar anatomical features of the most complete skull are discussed. The diagnostic characters of *Mystriosuchus* species B and the distinction from the type species are outlined.

To complete the systematic part, chapter 4 reviews the status of the taxa *Phytosaurus cylindricodon*, *Phytosaurus cubicodon*, *Belodon plieningeri*, and *Belodon ingens*. The first three taxa are considered *nomina dubia*; *Belodon ingens* is a *nomen nudum*.

In chapter 5, the preliminary results of a cladistic analysis of phytosaur taxa at species level are presented, based on the descriptions presented in chapters 2 and 3, and data from the literature. The focus of the analysis is on the controversial position of the genus *Mystriosuchus*, and the monophyletic status of the most primitive phytosaurs, that have been suggested in previous phylogenetic hypotheses.

Abbreviations

Institutions housing material used or referred to in this study:

AMNH = American Museum of Natural History, New York, U.S.A.
BMNH = The Natural History Museum, London, UK.
FSF = Forschungsinstitut Senckenberg, Frankfurt/Main, Germany.
GPIT = Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany.
HMB = Museum für Naturkunde der Humboldt-Universität Berlin, Germany.
MBSN = Museo Civico di Scienze naturali "E. Caffi", Bergamo, Italy.
MCZ = Museum of Comparative Zoology, Harvard University, U.S.A.
NMW = Naturhistorisches Museum Vienna, Austria.
RME = Ruhrlandmuseum Essen, Germany.
SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany.

Other abbreviations used in the text:

uncat. no. = uncatalogued or catalogue number lost, followed by a serial manuscript number.
unnumb. = catalogue number not given.

Chapter 2

Nicrosaurus

Section 2.1
The genus *Nicrosaurus* O. FRAAS, 1866

2.1.1 Systematic palaeontology

Archosauria COPE, 1869
Crurotarsi SERENO et ARCUCCI, 1990
Phytosauria JAEGER, 1828 (*sensu* DOYLE & SUES 1995)
Phytosauridae JAEGER, 1828 (*sensu* DOYLE & SUES 1995)

Nomenclatural remark: DOYLE & SUES (1995) credited the family group name Phytosauridae to MEYER, 1861, based on article 11f(iii) ICZN. The reasoning given for not crediting the first author to latinise the nomen (LYDEKKER 1888) is correct. However, the existence of a higher-level group was first suggested by JAEGER (1828: 44), in a latinised form although with an incorrect family ending:

> "Presumably at a time when more remains of those animals have accumulated, it will be possible to decide, whether aforementioned species [*Cylindricodon* and *Cubicodon*] stand apart as special genera or can be grouped perhaps with *Iguanodon* and several Extant reptiles *at least in a family* of plant-eating reptiles, for which I suggest the name *Phytosaurus*". (my translation and italics)

Thus, it is expressed *in litteris* that *Phytosaurus* was not intended as a generic name, but meant a higher category grouping at or even above family rank. Actually, both is now the case - *Phytosaurus* is an available generic name (though invalid, see section 5.1) and Phytosauridae is a generally accepted family (though neither herbivorous nor particularly close to ornithischians and monitor lizards). I follow article 36a ICZN (DOYLE & SUES 1995) in giving the credit for Phytosauria to the same author.

Genus *Nicrosaurus* O. FRAAS, 1866

Type species: *Nicrosaurus kapffi* (MEYER, 1860), by indication in FRAAS (1866) in accord with Art. 68(d) ICZN (monotypy)

Species included: "*Belodon plieningeri*" *sensu* MEYER (1861), here referred to as *Nicrosaurus* species B

Unassigned specimens, referred to *Nicrosaurus* sp. indet.:
BMNH 38037, skull lacking most of the snout
BMNH 38042, isolated postorbito-squamosal bar

Synonyms:
Phytosaurus JAEGER, 1828 [partim]
Belodon MEYER, 1844 [partim]
Lophoprosopus MEHL, 1915

Summary description: Moderately large genus (maximum skull length 900 mm) of Phytosauridae showing the following characters: usually at least a short prenarial crest present; nares below the level of the skull roof; anterior rim of the naris at or somewhat behind the level of the anterior rim of the antorbital fenestra; elongate depressed area on the lacrimal linking the orbit and the antorbital fenestra; small, sometimes deep external pre-infratemporal recess; supratemporal fenestra moderately wide, subrectilinear with rounded anterior margin; descending squamosal processes of the parietals meet in an angle ("inverted V"-shape of previous authors); parieto-squamosal bar depressed below the level of the skull roof for a distance of approximately 20 to 25% of the skull height; postorbito-squamosal bar relatively broad and short, thin dorsoventrally; medial part of the postorbito-squamosal bar overhangs the lateral half of the supratemporal fenestra; vertical component of the squamosal body narrow; posterior process of the squamosal not continuously tapering in dorsal view; suborbital opening long and slit-like (partially); palatine visible on the palatal vault in ventral view; ectopterygoid canal or ectopterygoidal excavation absent; pterygo-quadratal plate sloping anterolaterally; quadrate wing of the pterygoid bifurcated (?).

Suggested diagnostic characters (see discussion in subsection 2.1.2):

(1) a deep infranasal recess on the snout flank that separates the narial region from the antorbital fenestra and continues further forward along the nasal-maxilla suture.

(2) medial wings of the palatines meet at the midline of the palatal vault.

Tentatively suggested diagnostic character (see discussion in subsection 2.1.2):

(3) foramen nervi hypoglossi integrated into the recess of the foramen jugulare (not positively identified in *Nicrosaurus kapffi*).

Distribution: central and northern Württemberg, Southwest Germany.

Stratigraphic range: Upper Triassic, Keuper succession, Middle Keuper, Stubensandstein, lower (?) and middle Stubensandstein.

Age: Early (to Middle?) Norian, Late Triassic.

In the following sections, I will demonstrate that, apart from the snout profile, there are mostly gradual differences between the skulls of *Nicrosaurus kapffi* and "*Belodon plieningeri*, which do not merit generic separation according to our current understanding of the composition of a phytosaur genus. If we would accept such differences as standards for generic characters, we would necessarily be forced to split other well established and universally accepted higher taxa (like *Pseudopalatus* and *Mystriosuchus*, and probably even species among them) into a number of separate genera. The monogeneric assignment is confirmed here by the suggestion of two autapomorphies and one apomorphy in need of corroboration, which unites the species *kapffi* and "*Belodon plieningeri*" in the monophylum *Nicrosaurus*. The status of the "*Belodon plieningeri*" assemblage showing these autapomorphies is discussed in section 2.3. Meanwhile, the specimens are referred to in open nomenclature as *Nicrosaurus* species B.

2.1.2 The diagnostic characters of *Nicrosaurus*

(1) deep infranasal recess on the snout flank that separates the narial region from the antorbital fenestra and continues further forward along the naso-maxilla suture; [infranasal recess absent].

In *Smilosuchus gregorii*, the same type of surface sculpture as in *Nicrosaurus* may occur medial to the antorbital fenestra (LONG & MURRY 1995: figs. 27D, 29A), but these specimens clearly do not show a deep infranasal recess. The absence of an infranasal recess in all other crested or partially crested forms demonstrates that this excavation is

not a structural requirement of the prenarial crest, and the presence in *Nicrosaurus* species B suggests that it is also not linked with functional necessities related to a massive rostrum or laterally expanded snout. While its function is presently unknown, the infranasal recess seems to be a morphogenetically independent feature of *Nicrosaurus* that is unique among post-Carnian phytosaurs. It is paralleled in *Francosuchus angustifrons* and to a lesser degree in *Ebrachosaurus neukami* (KUHN 1936: pl. 10 fig. 5, pl. 8 fig. 1a).

(2) medial wings of the palatines meet in mid-line of the palatal vault; [palatines well separated on the palatal vault].

In both species of *Nicrosaurus*, the suture between the palatine and the pterygoid is visible on the anterior part of the palatal vault in ventral view. The medial wings of the palatines approach each other and finally achieve contact behind the vomers. This is in contrast to the majority of phytosaurs in which this region is adequately known ("*Parasuchus*": CHATTERJEE 1978, *Paleorhinus* DUTUIT 1977b; *Angistorhinus*: DUTUIT 1977a, MEHL 1913; *Brachysuchus*: CASE 1929 *Rutiodon carolinensis*: DOYLE & SUES 1995; *Leptosuchus adamanensis*: CAMP 1930; *Smilosuchus*: CAMP 1930). In all these forms, the pterygoids are apparently the only bones that form the roof of the palatal vault, and the medial wings of the palatines are either not present on the roof at all, or fully obscured from ventral view by the overhanging palatine ridges.

Two arguments might be put forward against an interpretation of this character state as a diagnostic character of *Nicrosaurus*:

Firstly, a remarkable exception within the aforementioned taxa is apparently found in *Leptosuchus crosbiensis*. According to CASE (1922: fig. 25C), the palatines in the type specimen unite broadly between and posterior to the choanae, and thus the vomers do not appear on the surface of the palate at all. Since *Leptosuchus crosbiensis* is the genotype, this peculiar feature would have to be included in the generic diagnosis. The medial extent of the palatines leads to such a unique configuration among phytosaurs, that I very much doubt the validity of CASE's reconstruction. My view is also supported by the fact that CASE (1929) later re-interpreted the choanal region of this specimen. In this subsequent reconstruction (CASE 1929: fig. 16), the vomers form the interchoanal septum as in all phytosaurs. It remains, however, unclear from this figure whether the palatines met in the mid-line of the palatal vault.

The second objection is that, in a number of the descriptions (CHATTERJEE 1978; DUTUIT 1977a; LEES 1907; MEHL 1913) it is not absolutely clear how far the reconstructions of the palatal vault are based on genuine observations, or whether the interpretations were improved according to a prevailing paradigm. It is my experience,

that the sutures on the palatal vault are difficult to discern because the bones are extremely delicate in this region and the bone surfaces tend to crushing and flaking. The connection of the palatines along the mid-line of the palatal vault can be demonstrated fairly accurately and reliably only twice in *Nicrosaurus*, the other specimens being inconclusive. Indeed, there are many descriptions not listed above, in which the authors express a greater or lesser great degree of uncertainty about the configuration of palatines, pterygoids, and vomers (e. g. CASE, 1922; CASE & WHITE 1934; MCGREGOR 1906; MEHL 1922, 1928; LANGSTON 1949). It therefore cannot be excluded that a similar palatal configuration as described for *Nicrosaurus* here is actually present in other genera as well, but still unrecognised. For the time being, I consider the condition as autapomorphic.

(3) foramen nervi hypoglossi (XII) located in the recess leading into the foramen jugulare; [foramen situated on the lateral face of the exoccipital pillar, well apart from the foramen jugulare].

In the best known examples of phytosaur braincases, one specimen each referable to "*Parasuchus*" (CHATTERJEE 1976: fig. 5c) and *Smilosuchus* (CAMP 1930: figs. 37, 46), a pair of foramina nervi hypoglossi is well separated from the foramen jugulare and is visible in lateral view on the exoccipital pillar posterior to the foramen jugulare. The same condition is indicated in an endocranial cast of *Leptosuchus* sp. (CASE 1928), as well as in CAMP's (1942: fig. 21) figure of the internal aspect of the braincase of *Machaeroprosopus zunii* (= *Leptosuchus adamanensis*, according to LONG & MURRY 1995).

The primitive *Francosuchus* shows also a laterally placed, but singular hypoglossal foramen (KUHN 1936). In *Mystriosuchus*, a singular foramen nervi hypoglossi and the foramen jugulare are closer together than in the aforementioned genera, but still well separated (HUENE 1911). Since the number of hypoglossal foramina is generally highly variable among species and higher categories (ROMER 1956), a distinction based on this character is not advisable.

The character state as defined above is clearly expressed in *Nicrosaurus* species B (BMNH 42745; subsection 2.3.2, Fig. 2.58) with the result that the (singular) foramen is not visible in lateral view on the braincase any more. The position of the foramen nervi hypoglossi is admittedly not known in *Nicrosaurus kapffi*; however, no foramen (or foramina) that can be attributed to the nervus hypoglossus is found on the lateral face of the exoccipital. It must be noted, however, that *Angistorhinopsis ruetimeyeri*, which is, according to the data presented in HUENE (1922), a more derived taxon than *Nicrosaurus* in having vertically descending squamosal processes of the parietals, shows both character states: a singular hypoglossal foramen separated by a thin lamina from the

foramen jugulare, but clearly within the jugular recess (HUENE 1922: fig. 114f). No data is available for *Pseudopalatus* and *Arribasuchus*. Hence, there is the possibility that the position of the foramen is characteristic of a more inclusive ingroup within Phytosauria. As long as the data in *Angistorhinopsis* has not been reexamined and confirmed, I consider the derived character state as autapomorphic for *Nicrosaurus*.

2.1.3 Non-European *Nicrosaurus*?

Numerous authors have postulated or quoted the occurrence of the genus *Nicrosaurus* outside Southwest Germany. Disregarding earlier citations, the number of recent advocates is rather impressive, including GREGORY (1962a, 1969), WESTPHAL (1976), LUCAS *et al.* (1985), CHATTERJEE (1986), MURRY (1986), LUCAS & HUNT (1989), MURRY (1989a), MURRY & LONG (1989), PARRISH (1989), SMALL (1989), SHUBIN & SUES (1991), HUNT (1993a), and HUNT & LUCAS (1993b), who all named *Nicrosaurus* as a component of the semiaquatic terrestrial fauna of the Chinle Formation and the Dockum Group in the southwestern United States. Moreover, *Nicrosaurus* was identified on the Indian subcontinent (KUTTY & SENGUPTA 1989; BENTON 1993; SENGUPTA 1995; LOYAL et al. 1996). For various reasons, it is of great importance to review and scrutinise the arguments on which the presence of *Nicrosaurus* in the Upper Triassic outside Europe is based. A positive identification in the fossiliferous North American deposits, for example, would be of outstanding significance for the biostratigraphic correlation of continental Upper Triassic deposits, which are notoriously difficult to compare by other means. Furthermore, producing compelling evidence of the presence of *Nicrosaurus* elsewhere would probably require us to modify our current hypotheses regarding the palaeobiogeography and the faunal interchange between terrestrial environments in Late Triassic times.

The type species of the genus *Nicrosaurus* is *Nicrosaurus kapffi*. It is a simple fact that a character not expressed in the type species cannot be claimed as diagnostic for the genus. The character states that have been used to define *Nicrosaurus* in the past (mostly with the intention to incorporate non-European species) must be present in the specimens referred to *Nicrosaurus kapffi* to fulfil the claim of being valid diagnostic characters. Furthermore, a generically diagnostic character must occur in all species that are referred to that genus. In the more strict sense of cladistics which is adopted here, any operational taxonomic unit deemed a species separate from the species *kapffi* must show derived

characters unique to that species and *Nicrosaurus kapffi* to be unequivocally included in the genus.

In 1962, GREGORY considerably extended the definition of the genus *Nicrosaurus* (first under the now invalid genus-name *Phytosaurus*, which he later synonymised with *Nicrosaurus* in GREGORY 1969) by introducing 11 distinctive characters, in order to achieve a "simpler and more meaningful classification" (GREGORY 1962: 652) of phytosaurs.

A closer examination shows that GREGORY's (1962a: 680) character state (4) "posterior process of squamosal deeper than long", and (11) "suborbital fenestra small" do not apply to the type species of *Nicrosaurus*, but are obviously based on the more primitive phytosaur *Smilosuchus gregorii*. Most of the other characters are formulated in such a general way that they fit to a variety of readily distinguishable phytosaur taxa. Character (1) "external nares between antorbital fenestrae" and (2) "posterior border of supratemporal fenestra depressed" define more inclusive groups than *Nicrosaurus* (BALLEW 1989; chapter 5). Moreover, the definition of narrowness in "supratemporal fenestra narrow", also included in character (2), is arbitrary; at least one taxon with much narrower supratemporal fenestrae than *Nicrosaurus* (*Arribasuchus buceros*) is not included. The large size of the posttemporal fenestra (character 3) is a plesiomorphic trait among Phytosauridae (chapter 5). Character state (5) "upper temporal bar continuously round" (i.e. no squamosal ridge present) applies to all Phytosauridae except *Mystriosuchus* (BALLEW 1989). The wordings of characters (6), (7), and (10) (including the orientation of the orbits, the height of the quadrate, and the nature of the dentition) is identical with the diagnosis of "*Rutiodon*" presented in the same paper, and the characters are thus not diagnostic for "*Phytosaurus*". Furthermore, the orientation of the orbits and the skull height are found to be variable in *Nicrosaurus kapffi* (subsection 2.2.5). The constant ratio of prenarial to postnarial skull length (character 9; given as 1.22, but ranging from 1.17 to 1.36 in GREGORY 1962a: fig. 4) broadly characterises *Nicrosaurus kapffi* and *Smilosuchus gregorii*, but applies also to *Angistorhinus talainti*, *Brachysuchus megalodon* and *Leptosuchus crosbiensis* (Tab. B.1). *Angistorhinus talainti* and *Brachysuchus megalodon* belong to the more primitive clade Angistorhininae (BALLEW 1989; chapter 5), and *Leptosuchus crosbiensis* was not included in "*Phytosaurus*" by GREGORY, but in "*Rutiodon*". Character (8), first defined as "rostrum massive bearing a swollen dorsal crest throughout its length", becomes ambiguous by the specification "...or evenly descending profile from external nares to rounded tip" (GREGORY 1962a: 683).

The result of GREGORY's redefinition was an accumulation of typologically similar species with massive snouts, with or without prenarial crests, and including *Nicrosaurus*

kapffi, *Smilosuchus gregorii*, and *Brachysuchus megalodon*, that are now unanimously regarded as representatives of at least three separate genera (BALLEW 1989; HUNT 1994; LONG & MURRY 1995). Even when *Brachysuchus* was later excluded (GREGORY 1969), most of the inconsistencies in the diagnosis of *Nicrosaurus* prevailed. However, the simplicity of GREGORY's concept proved highly influential, and the majority of the named subsequent references claiming an occurrence of *Nicrosaurus* in North America can be traced back to GREGORY's (1962a, 1969) studies.

PARRISH (1989: 363) defined *Nicrosaurus* as having an "essentially flat horizontal surface of skull roof and crest, an elongate antorbital fenestra that opens anterodorsally, and a broad snout with ventrally expanded posterior premaxillaries". The meaning of a flat horizontal surface is unclear to me. Interpreted as "straight prenarial crest", it would apply to *Nicrosaurus* (*kapffi*), but to none of the North American taxa. Focusing on the flat (i.e. not sharp) surface of the crest, this is also present in *Smilosuchus*, but in this taxon, the crest top is not horizontal. The invalidity of the second character is shown in part 2.2.5.3. The expanded premaxillaries occur in several heterodont phytosaur species, which do not form a natural group (including even a species of *Paleorhinus*, LONG & MURRY 1995).

MURRY & LONG (1989) presented their interpretation of diagnostic characters in *Nicrosaurus*. Note that the authors included the specimens of "*Belodon plieningeri*" as the probably female morph of *Nicrosaurus kapffi*. Diagnostic characters given include: wide, short (length not more than six times the width), and prominently sculptured postorbito-squamosal bar; squamosal triangular in lateral view and pointed; lateral groove on squamosal. Based on this diagnosis, "*Belodon*" *buceros* (including *Machaeroprosopus validus*, *Machaeroprosopus tenuis*, *Machaeroprosopus andersoni*, and *Pseudopalatus pristinus*) was referred to *Nicrosaurus*. *Nicrosaurus kapffi* shows no lateral squamosal groove and a rounded squamosal tip, rendering these characters invalid for the genus. BALLEW (1989) demonstrated that the remaining character states indeed define a clade, characterised by node M in her phylogenetic hypothesis, but the unnamed clade is more inclusive and most of the taxa included by MURRY AND LONG (1989) are valid and more derived than *Nicrosaurus kapffi*.

HUNT (1993a) and HUNT & LUCAS (1993b) also regarded "*Belodon*" *buceros*, but the type only, as the North American representative of the genus *Nicrosaurus*. In the first paper, *Nicrosaurus* is based on (1) depressed supratemporal fenestrae, which are described as being (2) slit-like, on (3) a wide postorbito-squamosal bar, and on (4) the position of the nares below the level of the skull roof. Again, the characters (1) and (3)

constitute more inclusive clades (BALLEW 1989; LONG & MURRY 1995), whereas character (4) is a symplesiomorphy of all phytosaurs except *Angistorhinus alticephalus*, *Pseudopalatus*, and *Arribasuchus*. Character state (2) does neither apply to *Nicrosaurus kapffi* nor to the specimens considered here *Nicrosaurus* species B.

It is most unfortunate that the type of the species "*Belodon*" *buceros* (AMNH 2318) was never adequately described, and thus the diagnostic characters of *Nicrosaurus* suggested here cannot be fully checked by comparison with published data. It is, however, evident that AMNH 2318 does not show an infranasal recess (HUENE 1915a: fig. 11; LONG & MURRY 1989: fig. 42D). BALLEW (1989) and LONG & MURRY (1995) additionally listed a number of features of "*Belodon*" *buceros* which are not present in the European *Nicrosaurus*, but in the more derived *Pseudopalatus* (and partially also in *Mystriosuchus*): most significant are the rounded shape (termed " inverted U-shaped") of the parietal-supraoccipital complex and strongly elongated posterior processes of the squamosals which taper over their whole length.

The occurrence of *Nicrosaurus* in the Dharmaram Formation of India can be readily dismissed because of insufficient evidence. All of the more recent references can be traced down to a study by KUTTY & SENGUPTA (1989). However, according to them, the identification of *Nicrosaurus* is based on material apparently insufficiently preserved for determination. Consequently, it is referred to, *in litteris*, as a "possible *Nicrosaurus*" (KUTTY & SENGUPTA 1989: 201), perhaps meaning a "*Nicrosaurus*-grade" phytosaur in the definition of GREGORY (1962a). Among the specimens is also provisionally included the type of the *nomen dubium* ?*Brachysuchus maleriensis* HUENE, 1940, which has already been referred earlier to *Nicrosaurus* (as *Phytosaurus maleriensis*) by GREGORY (1958). It is somewhat unfortunate and certainly misleading that later authors quoted KUTTY & SENGUPTA's aptly cautious identification in a way that suggests a secure determination.

Section 2.2
Nicrosaurus kapffi (MEYER, 1860)

2.2.1 History of taxonomy and research

Pending a decision on the debatable status of *Rutiodon carolinensis* EMMONS, 1856 (DOYLE & SUES 1995), the species *Nicrosaurus kapffi* represents the oldest proposed name for a phytosaur that is still considered valid to date. The species name was erected by the eminent German palaeontologist Hermann von MEYER in a published research letter (MEYER 1860b) as the second species of his phytosaur genus *Belodon*. He based the species on two snout fragments, of which the more informative one (SMNS 4060) was recovered by the private collector Sixt Friedrich Jakob von KAPFF in 1859 from a quarry near Heslach in the vicinity of Stuttgart. However, the syntype material includes also a specimen that had been collected from Löwenstein in North Württemberg, the type locality of *Belodon plieningeri*, about ten years earlier (KURR 1852) and previously had been misidentified as a part of a lower jaw of *Belodon plieningeri* (PLIENINGER 1857). This specimen, SMNS 54708, is the earliest find of a phytosaur that is specifically determinable.

Already a few years later, Oscar FRAAS (1866) proposed the new genus name *Nicrosaurus* explicitly to receive *Belodon kapffi*, because he felt uneasy about the incomplete nature of the type specimens of both the other available German phytosaur genera, *Phytosaurus* JAEGER, 1828 and *Belodon* MEYER, 1844. However, researchers disregarded FRAAS' generic name until quite recently, probably because the name *Belodon* was already so firmly established or because they were not aware of the name since FRAAS published his suggestion in passing in a popular book.

Compared to the majority of phytosaur taxa, the status of the species *Nicrosaurus kapffi* as well as the individual specimens assigned to the taxon remained largely unchanged. It was only ABEL's (1923) view on sexual dimorphism in phytosaurs that led him to group all Norian phytosaurs from Germany together into a single species, "*Phytosaurus kapffii*", of which he regarded the specimens of *Nicrosaurus kapffi* as males. Such a radical opinion was not accepted by subsequent workers. Other inconsistencies in the nomenclature of the *Nicrosaurus kapffi* can largely be attributed to two reasons. There is the varying opinion of individual workers, whether *Nicrosaurus kapffi* should be regarded as a junior synonym of *Phytosaurus cylindricodon* JAEGER,

1828, the first phytosaur to be named. In the case of a positive decision, however, numerous authors then chose to retain illegally the already well established and popular species name *kapffi* (CAMP 1930; CASE 1922, 1929; GREGORY 1962a, 1962b; HUENE 1911, 1922; MCGREGOR 1906; MEYER 1861). A second highly influential as well as controversial aspect for a long time was the practice of assigning rectangular dermal scutes, which have been found at the Heslach sites, to *Nicrosaurus kapffi*. It was not until 1985, when LONG & BALLEW identified these scutes as actually belonging to an aetosaur they named *Paratypothorax andressi*. The atypical nature of the alleged armour for a phytosaur convinced a number of workers of the validity of the species *Nicrosaurus kapffi*, or it was the decisive reason for others to separate *Nicrosaurus kapffi* generically from contemporaneous phytosaurs (CAMP 1930; GREGORY 1962a, 1969; GREGORY & WESTPHAL 1969; HUENE 1911; WESTPHAL 1976). As a matter of fact, no articulated skeleton of *Nicrosaurus kapffi* has ever been found, and it is even impossible to determine in retrospect, which of the numerous postcranial elements, or if any at all, have been collected in direct association with skulls. Thus all assignments of postcrania to *Nicrosaurus* (HUENE 1913, 1922; KREBS 1965; WESTPHAL 1976; GALTON 1985b) must be regarded as speculative and unjustified by evidence.

In his monograph on Stubensandstein reptiles, MEYER (1861) described the syntype series of *Nicrosaurus kapffi* (SMNS 4060, SMNS 54708), skull fragment 54706, and the mandible SMNS 4380 in detail. KAPFF's find of SMNS 4378 enabled MEYER (1863) to publish a thorough description of the skull. Here, a reconstruction of an almost complete phytosaur skull was presented for the first time. Numerous osteological details, like the depressed parieto-squamosal bar, that characterise the more derived phytosaurs, were correctly identified. Even after more than a century, this account is still the most useful anatomical study of *Nicrosaurus kapffi* to date. MEYER's declining health, which finally led to his untimely death in 1869, prevented him from completing further studies on *Nicrosaurus kapffi* that were already in preparation (MEYER 1866). Despite the abundance of more informative material that was recovered by KAPFF in the 1860's and 1870's, *Nicrosaurus kapffi* received little further attention. KOKEN (1888) mentioned in passing, for the first time, the presence of an ectopterygoid. MCGREGOR (1906: fig. 4) illustrated more accurately than MEYER the skull in posterior aspect, however, it is an idealised reconstruction most likely based on skull SMNS 4379. HUENE (1909, 1911) correctly demonstrated the presence and shape of a septomaxilla, but also added some confusion by misinterpreting the configuration of the pterygo-quadratal suture. In summary, there is still a considerable lack of anatomical information in *Nicrosaurus kapffi* regarding the palate, the temporal region, and the braincase and occipital region because of the incomplete preservation of SMNS 4378.

A synthesis of the skull osteology of *Nicrosaurus kapffi* is presented here, based on information from all the specimens available, together with illustrations of the material kept in the SMNS and BMNH. The monophyletic status of the species *Nicrosaurus kapffi* is supported by two autapomorphies (see part 2.2.6.1). Moreover, since *Nicrosaurus kapffi* is known from five almost complete skulls, three snouts, and two postorbital skull fragments, the fossil record is remarkably good compared to the majority of phytosaur species. For these two reasons, *Nicrosaurus kapffi* provides an opportunity to study the intraspecific variability of these cranial characters which are frequently estimated as diagnostically important. By extrapolation, the results may lead to important conclusions concerning the usefulness of a number of character states or skull features that are currently used to reconstruct the phylogeny of phytosaurs. Secondly, an attempt is made to distinguish between the underlying reasons of the character variability. The sample size, however, is far from statistically significant, but allows some tentative suggestions regarding character states or traits of character changes that may represent sexual dimorphism, individual variation, and ontogenetically governed changes. I hope, that the study of variation in a clearly monophyletic phytosaur species and elimination of intraspecifically variable character states will help to achieve a more stable alpha taxonomy of phytosaurs in general, and will contribute towards a more firmly based phylogenetic hypothesis.

2.2.2 Systematic palaeontology

Synonymy:

Nicrosaurus kapffi (MEYER, 1860)
(Figs. 2.1-2.44)

1852 Kieferstück mit mehreren Zähnen – KURR: p. 68.

1847-55 *Belodon Plieningeri* – MEYER [partim]: p. 148 "von Affalterach bei Löwenstein....Kieferfragmente" [= SMNS 53708], ? p. 148 "Quenstedt (1851-52: pl. 8 fig. 5)" [= Phytosauridae indet.], non p. 148 pl. 20 figs. 2-3 [= *Belodon plieningeri* MEYER, 1844], non p.148 pl. 20 figs. 4, 6-10 [= Phytosauridae indet.], non p. 149 [= *Plateosaurus engelhardti* MEYER, 1837, Phytosauridae indet.].

v 1857 *Belodon Plieningeri* H. von Meyer – PLIENINGER [partim]: p. 440, 446, pl. 8 fig. 1, ? pl. 8 figs. 3-6, 17-36, [= Phytosauridae indet.], non pl. 8 fig. 2 [=

Phytosauridae, non *Nicrosaurus kapffi*] non pl. 8 figs. 7-15 [= Archosauria indet.], non pls. 9-13 [= *Plateosaurus engelhardti* MEYER, 1837], non p. 389-392 [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non p. 458 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 458 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*].

1860 *Belodon Plieningeri* – MEYER [partim]: p. 212 "in mehreren Schädeln vorliegend". [1860a].

*v 1860 *Belodon Kapffi* – MEYER: p. 556. [1860b].

1861 *Phytosaurus* Jäger 1826 [sic] – O. FRAAS [partim]: p. 101 [KAPFF's finds, partim], non p. 101 "Rübgarten" [= *Phytosaurus* JAEGER, 1828, *nomen dubium*], non p. 101 "Saurierreste von Löwenstein, Affalterach, Leonberg, Aixheim" [= MEYER (1847-55), PLIENINGER (1857), QUENSTEDT (1851-52)].

v 1861 *Belodon Kapffi* [p. 346: *Belodon Kapfii*] Meyer – MEYER [partim]: p. 346, p. 284, pl. 30, pl. 31 fig. 9-12, pl. 32, pl. 33 figs. 1-2, pl. 35 fig. 1, pls. 46-47, ?pl. 31 figs. 6-7, ?pl. 34 figs. 1-4, ?pl. 37 fig. 14, ?pl. 34 fig. 7, non pp. 295, 346 "Cylindricodon JAEGER, 1828, Cubicodon JAEGER, 1828" [= *Phytosaurus cylindricodon* JAEGER, 1828, and *Phytosaurus cubicodon* JAEGER, 1828, *nomina dubia*].

1862 *Belodon Kapffi* – MEYER: p. 333.

v 1863 *Belodon Kapffi* Meyer – MEYER: p. 227, pls. 38-40, pl. 42 figs. 1-5.

1864 *Belodon Kapfii* H. v. MEYER [sic] – ALBERTI [partim]: p. 229 footnote, non p. 229 footnote "v. JAEGER (1828: pl. 6 figs. 13-15)" [sic] [= *Phytosaurus cylindricodon* JAEGER (1828), *nomen dubium*], non p. 229 footnote "v. JAEGER (1828: pl. 6 figs. 17-22)" [sic] [= *Phytosaurus cubicodon* JAEGER (1828), *nomen dubium*].

1864 *Belodon Kapffi* – MEYER: p. 211.

1864 *Belodon Kapffi* o. M. [sic] – KAPFF: p. 33.

1865 *Belodon Kapffi* – MEYER: p. 221. [1865a].

1865 *Belodon Kapffi* – MEYER: p. 112. [1865b].

1865-66 *Phytosaurus cylindricodon* – QUENSTEDT [partim]: p. 133, pl. 9 fig. 1 [modified after MEYER (1863)], non fig. 46 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*], non fig. 47 [= *Mystriosuchus planirostris* (MEYER, 1863)], non p. 134 "Schilder" [= *Paratypothorax andressi* LONG & BALLEW], 1985, non p. 135 [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*].

1866 *Belodon Kapffi* – MEYER: p. 576.

v 1866 *Nicrosaurus Kapffii* v. Meyer [sic] – O. FRAAS: p. 210, fig. 75 top and right, fig. 76, ?fig. 75 bottom [according p. 211 composite, number of toes and phalanges fictional].

1870 *Belodon* – HUXLEY [partim]: p. 39, 40

1872 *Phytosaurus Kapffii* [sic] – SCHEMPP: p. 212.

non 1875 *Belodon Kapffi* – KAPFF: p. 303 [= *Paratypothorax andressi* LONG & BALLEW], 1985].

1875 *Belodon* – HUXLEY [partim]: p. 426.

1877 Saurierreste – O. FRAAS [partim]: p. 2.

1882-85 *Phytosaurus cylindricodon* Jaeger 1828 – QUENSTEDT [partim]: p. 17, pl. 13 fig. 1 [cop. MEYER 1863], ? "cf. Belodon Kapffi" pl. 14 figs. 7-9, non fig. 57 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non fig. 58 [= *Mystriosuchus planirostris* (MEYER, 1863)].

? 1882-85 *Teratosaurus suevicus* MEYER – QUENSTEDT [partim]: p. 181, ? pl. 14 figs. 4-5, non pl. 14 fig. 6 [= ?*Teratosaurus suevicus* MEYER, 1861].

1887 *Belodon* – KOKEN [partim]: p. 96.

1887-90 *Belodon kapffi* H. v. MEYER – ZITTEL [partim]: p. 638 figs. 561, 562 [modified after MEYER 1863], ? p. 642 fig. 568b "Seitenplatte" [Phytosauria indet., modified after MEYER 1861], non p. 642 fig. 568a [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1888 *Belodon* – KOKEN [partim]: p. 764.

v 1888 *Phytosaurus cylindricodon*, Jäger 1828 – LYDEKKER [partim]: pp. 124, 125 "BMNH 39477" [= cast of SMNS 4379, not SMNS 4378 MEYER (1863: pls. 38-40)], "BMNH 42743, 38043, 38036, 42744", fig. 17, ? p. 125 "BMNH 38037" [= *Nicrosaurus* sp.], ? p. 126-128 [postcranial elements], non p. 125 "BMNH 38039" [= *Nicrosaurus* species B], non p. 125 "BMNH 38042" [? *Nicrosaurus* species B]. non p. 125 "BMNH 38040" [= rauisuchian cf. *Teratosaurus suevicus* MEYER, 1861], non p. 126 "BMNH 27994" [? cast of mandibular tip of *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*].

1889 *Phytosaurus* – QUENSTEDT [partim]: pp. 120, 128, ? p. 129, non p. 120 [= *Belodon plieningeri* Meyer, 1844, *nomen dubium*].

1893 *Belodon kapfii* [sic] – COPE: p. 13

1896 *Belodon Kapffii* H. v. MEYER [sic] – E. FRAAS [partim]: p. 15, pl. 5 right, ? p. 15 [postcrania, = Phytosauria indet.], ? p. 17 [coracoid, = Phytosauria indet.], non p. 16 "Hautschilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1896 *Belodon Kapffi*, von Meyer – MARSH: p. 62, fig. 3.

1888 *Belodon Kapffii* [sic] – E. FRAAS: p. 4.

1900 *Belodon Kapffii* [sic] – E. FRAAS: p. 511, 513.

1906 *Phytosaurus Kapffi* (H. von MEYER) – MCGREGOR [partim]: p. 93, fig. 4, pl. 11 fig. 47, tab. fig. 1: no. 4-5, pp. 37, 38, 39 "teeth", 40, 42, 47 "length of symphysis", 49 "number of mandibular teeth", ? pp. 51, 52, 54, 56, 57 "Meyer (1863: pl. 44 fig. 4)", 64, 67 "Meyer (1965: pl. 33 figs. 1-3)", 72, 74, non p. 93 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 93 [= *Phytosaurus cubicodon* JAEGER, 1928, *nomen dubium*], non p. 56 "dermal armour" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1907 *Nicrosaurus Kapffi* Hermann von Meyer– ESER: p. 660.

1907 *Belodon kapffi* – LEES: pp. 122, 133, 136.

1908 *Belodon Kapffi* H. v. MEY. – ENGEL [partim]: pp. 172, 170, fig. p. 173, non p. 170 "Hautschilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985], non p.172 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 172 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*].

1909 *Phytosaurus Kapffi* (H. v. MEYER) – HUENE [partim]: pp. 585, 589, 592, non 592 [= *Belodon ingens* Fraas, 1896, *nomen nudum*].

1910 *Belodon* (*Phytosaurus*) *Kapffii* H. v. MEY. [sic]– E. FRAAS [partim]: p. 23, ? p. 23 [all postcrania], non p. 23 "Hautschilder" [probably = *Paratypothorax andressi* LONG & BALLEW, 1985].

1910 *Phytosaurus Kapffi* v. MEYER – JAEKEL: fig. 9.

1910 Belodon-Reste – LANG [partim]: p. 50 footnote 1.

v 1911 *Phytosaurus Kapffi* (H. v. MEYER) – HUENE [partim]: pp. 91, 120, figs. 12-16, non fig. 25 [= *Paratypothorax andressi* LONG & BALLEW, 1985], non p. 38, fig. 24/3, 8-13 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 38, fig. 24/17-20 [= *Phytosaurus cubicodon* JAEGER, 1928, *nomen dubium*].

? 1913 *Belodon Kapffii* [sic] – FRAAS: p. 1097. [1913b].

? 1913 *Phytosaurus Kapffi* (H. v. MEYER) – HUENE [partim]: figs. 2, 4-6, 8, 10, 12, non fig. 13 [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1914 *Belodon* – BOAS: p. 276, fig. 60 [cop. MCGREGOR 1906].

1914 *Belodon Kapffii* [sic] – FRAAS: p. 126.

non 1914 *Belodon kapffi* – SCHMIDT: p. 31 [= Phytosauria indet.].

1914 *Belodon kapfii* [sic] – WILLISTON: p. 185, fig. 96.

1915 *Phytosaurus kapffi* – HUENE [partim]: p. 491, ? p. 495 "tibia fig. MEYER (1861 [non 1859!]: pl. 42 fig. 1), non p. 492 "scutes" [= *Paratypothorax andressi* LONG & BALLEW, 1985]. [1915a]

1915 *Lophoprosopus* (*Belodon*) *kapffi* von MEYER – MEHL [partim]: p. 163, non p. 163 "*Zanclodon arenaceus* FRAAS, 1896' [= Phytosauria indet.], non p. 163 "*Belodon ingens* FRAAS, 1896" [= *nomen nudum*].

1916 *Lophoprosopus* (*Belodon*) *kapffi* – MEHL : pp. 7, 12, 14, 22.

1920 *Phytosaurus kapffi* – CASE: p. 533.

? 1920 *Phytosaurus kapffi* – HUENE: p. 144.

?v 1922 *Phytosaurus Kapffi* – HUENE [partim]: pp. 60, 146, 156, ? figs. 3-11, 14-17, 26-27, 30, 33, 37, 39, 41, 48, 51-52, 54, 58-64 [all postcrania], non fig. 29 [= *Teratosaurus suevicus* MEYER, 1861], non p. 145 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*].

1922 *Phytosaurus kappfi* [sic] – CASE: fig. 24D [cop. MCGREGOR 1906], non fig. 24E [= *Mystriosuchus planirostris* (MEYER, 1863)].

1923 *Phytosaurus Kapffii* MEYER [sic] – ABEL [partim]: p. 57, figs. 6-7, non fig. 1 [= *Mystriosuchus* species B], non fig. 2 [= *Mystriosuchus planirostris* (MEYER, 1863)].

1923 *Phytosaurus Kapffii* [sic] – HUENE: p. 369.

1928 *Phytosaurus kapffi* H v. MEYER – SCHMIDT [partim]: p. 415, fig. 1166 [modified after FRAAS 1896], ? fig. 1167 [postcrania, cop. HUENE 1922], ? fig. 1165b [pelvis, cop. HUENE 1902], non p. 415 [= *Belodon ingens* FRAAS, 1896, *nomen nudum*], non p. 415 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 415 figs. 1165a, 1169 [= *Phytosaurus cubicodon* JAEGER , 1828, *nomen dubium*], non fig. 1165a [= *Nicrosaurus* species B, non cop. JAEGER 1828, cop. MEYER 1861], non fig. 1168 [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1929 *Phytosaurus kappfi* [sic] – CASE [partim]: p. 23, 48, ? p. 50 "ilium Huene (1913: fig. 10)", non p. 43 "rectangular shaped plates" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1929 Belodon-Knochen – STOLL [partim]: p. 41.

1929 *Phytosaurus*-Reste – STOLL: p. 51.

1930 *Phytosaurus kapffi* (H. von MEYER) – CAMP [partim]: p. 141, fig. 6, ? p. 64ff [postcrania], non p. 138 "dorsal armour" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1931 *Phytosaurus* G. von JÄGER, 1828 – BERCKHEMER [partim]: p. 4, fig. 1, non p. 4 [= *Phytosaurus* Jaeger, 1828, *nomen dubium*].

1932 *Phytosaurus* – CASE: p. 74. [1932b].

1932 *Belodon kapffi* H. v. MEYER – ZITTEL [partim]: p. 346, fig. 448, non fig. 450 [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1933 *Phytosaurus kapffi* H. v. M. – KUHN [partim]: p. 18, non p. 18 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 18 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*].

1934 *Phytosaurus kapfii* [sic] – CASE & WHITE: p. 137.

1934 *Phytosaurus kapffi* – KUHN [partim]: p. I.

1935 *Phytosaurus* (*Belodon*) *kapffii* Meyer [sic] – ABEL: pp. 571, 573, fig. 472 [cop. MEYER 1863].

? 1936 *Phytosaurus kapffi* H. v. M. – KUHN: p. 86 [ilium], p. 89 [humerus, ulna], p. 92 [scapulacoracoid].

1947 *Nicrosaurus kapffi* (H. v. MEYER 1861) – COLBERT: tab. 1.

1953 *Phytosaurus kapffi* – GREGORY: p. 5

1954 *Phytosaurus kapfi* [sic] – HELLER: p. 11.

1955 *Phytosaurus kappfi* (Meyer) [sic] – HOFSTETTER: p. 690, fig. 11C, 16F [cops. MEYER].

1956 *Phytosaurus kapffi* – HUENE [partim]: p. 462, ? fig. 495b-c, non fig. 495a [= T*eratosaurus suevicus* MEYER, 1861], non p. 462 "Panzerung" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1961 *Phytosaurus kapffi* – KUHN: fig. p. 187 [cop. SCHMIDT 1928]. [1961a]

1961 *Phytosaurus kapffi* H. v. Meyer 1861 – KUHN: p. 96. [1961b]

1962 *Phytosaurus kapffi* – GREGORY [partim]: p. 6, 10, 11, 19, non p. 19 "dermal armour" [= *Paratypothorax andressi* LONG & BALLEW, 1985]. [1962a]

1962 *Phytosaurus kapffi* (MEYER, 1861) – GREGORY [partim]: p. 679, figs. 3B, 4, 5D, tabs. 1-4, non p. 679 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 679 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*], non p. 682 "rectangular scutes" [= *Paratypothorax andressi* LONG & BALLEW, 1985]. [1962b].

1963 *Nicrosaurus kapffi* – WESTPHAL: p. 121, figs. 1, 5 bottom [1963a]

1963 *Nicrosaurus kapffi* (H. v. MEYER 1860) – WESTPHAL [partim]: p. 164, 169, fig. 1 bottom, pl. 15 fig. 2, non p. 165 "rechteckige Rückenplatten" [= *Paratypothorax andressi* LONG & BALLEW, 1985]. [1963b].

1963 *Nicerosaurus* [sic] *kapffi* (H. v. MEYER 1860) – WESTPHAL : p. 22. [1963c].

non 1965 *Phytosaurus* – COLBERT: p. 16 "large type of scute" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

? 1965 *Belodon kapffi* – KREBS: tabs. 3, 5, 6, 9 [postcrania].

1965 *Belodon kapffi* – SWINTON: p. 77, fig. 44.

1968 *Nicrosaurus* (*Phytosaurus*) *kapffi* JAEGER – KUHN: p. 75, figs. 37, 5-6 [cops. ZITTEL 1887-90], ? figs. 35,8-10 [humerus, femur, ilium].

1968 *Belodon kapffi* – WALKER: p. 8.

1969 *Nicrosaurus kapffi* MEYER – GREGORY [partim]: p. 44, fig. 5, non p. 44 "Hautschilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1969 *Nicrosaurus kapffi* (Meyer 1860) – GREGORY & WESTPHAL [partim]: p. 1297, non p. 1297 "transversely widened scutes figured by MEYER (1861: pl. 43), MEYER (1865b: pl. 28)" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

non 1971 *Nicrosaurus kapffi* – KUHN: figs. 23, 28.

1971 *Nicrosaurus kapffi* MEYER 1861 – KUHN [partim]: p. 14, figs. 25(1), 25(13), 25 right half fig. 4, ? figs. 23(26-27) [humerus, femur], non p. 14 [= *Phytosaurus* JAEGER, 1828, non p. 14 *Cylindricodon* JAEGER, 1828, non p. 14 *Cubicodon* JAEGER 1828, *nomina dubia*].

1973 *Nicrosaurus kapffi* H. v. M. – BRENNER: p. 171, 183.

1976 *Nicrosaurus kapffi* (H. v. MEYER 1861) – WESTPHAL [partim]: p. 113, fig. 11 a, b, e, ? fig. 4a, g-j [postcrania], ? fig. 5a-c [postcrania], non fig. 11d [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1977 *Mystriosuchus* [*Belodon*] *kapffi* H. v. MEYER – STRÖBEL & WURM: p. 53.

1978 (Saurier-) Reste – BRENNER [partim]: p. 136. [1978a]

1978 *Nicrosaurus kapfi* (Meyer), 1860 [sic] – CHATTERJEE: p. 115, figs. 16f [cop. GREGORY 1969], fig. 18, tab. 3.

? 1985 ?*Nicrosaurus* – GALTON: p. 12, fig. 1D. [1985b].

1985 *Nicrosaurus kapffi* – LONG & BALLEW: p. 56.

1985 *Nicrosaurus kapffi* (H. v. MEYER)– MÜLLER [partim]: p. 314, fig. 379 [cop. FRAAS 1896], non fig. 381 [= *Paratypothorax andressi* LONG & BALLEW, 1985]

1986 *Nicrosaurus kapffi* – BUFFETAUT & WOUTERS: pp. 137, 138.

1986 *Nicrosaurus* – CHATTERJEE: p. 143.

1986 *Nicrosaurus* – ZIEGLER: p. 133, figs. 153-154.

1988 *Nicrosaurus* – ZIEGLER: p. 19, fig. 18.

1989 *Nicrosaurus kapffi* (v. MEYER, 1861) – BALLEW: p. 326.

1989 *Belodon Kapfii* [sic] – HUNT & LUCAS: pp. 340, 343, 346. [1989b].

1989 *Nicrosaurus* – PARRISH: p. 363.

1989 *Nicrosaurus* – WILD: p. 16.

1990 European *Nicrosaurus* – RUBEN: p. 527.

1991 *Nicrosaurus kapffi* (v. MEYER, 1861) – WILD: p. 60, figs. 46-47.

1993 '*Belodon*' – BENTON & WILD [partim]: p. 37 [term '*Belodon*' includes all phytosaurs from the Stubensandstein].

1994 *Nicrosaurus kapfii* [sic]– HUNT: 30A.

1994 *Belodon kappfi* [sic] – PARRISH: p. 207

1994 *Nicrosaurus kapffi* – WILD: p. 19, figs. 9-10.

1995 *Nicrosaurus kapffi* – HUNGERBÜHLER: p. 68, fig. 3, fig. p. 72 [cop. FRAAS 1866].

1995 *Nicrosaurus kapfii* (H. v. MEYER, 1861) [sic] – LONG & MURRY: p. 60, figs. 40C, 56A, B.

1996 "*Phytosaurus kapfii*" [sic] – GALTON & WALKER: p. 732.

1996 parasuchian teeth – GALTON & WALKER: p. 733 "figured by Meyer (1861: .... Pl. 46)".

1996 *Nicrosaurus kapffi* (MEYER, 1860) – HUNGERBÜHLER: p. 43A

1997 *Nicrosaurus kapffi* – GODEFROIT & CUNY: p. 7.

Nomenclatural remark: The species name is frequently spelled "*kapffii*", probably because of an apparent misspelling on page 346 in MEYER (1861), where he lists the specimens he attributed to the taxon. However, the species-group name was erected in the etymologically correct form (Article 33d ICZN) in MEYER (1860b) and is spelled like this in all his subsequent publications, except the place referred to above. Other ways of spelling such as: "*kapfi*", "*kapfii*", or "*kappfi*" are obviously transcription errors.

Lectotype (designated here):

SMNS 4060: badly corroded and damaged snout fragment, figured by MEYER (1861: pl. 30 figs. 1-3; pl. 33 fig. 1) and in Figure 2.3A-E. For measurements, see Table 2.2.1.

SMNS 4060a: posterior symphyseal and anterior postsymphyseal part of both mandibular rami found in occlusion with the snout SMNS 4060 (MEYER 1861: pl. 33 fig. 2; Fig. 2.3F).

SMNS uncat. no. 15: fragment of the posterior part of a left maxilla with parts of the jugal that fits to the snout SMNS 4060. Moreover, there is SMNS uncat. no. 14 from the former KAPFF collection, a corresponding fragment belonging to the right side of a skull, which additionally includes a portion of the ectopterygoid. The identical nature of preservation, and the corresponding dimensions of the fragment and its alveoli to SMNS uncat. no. 15 and SMNS 4060 may indicate that SMNS uncat. no. 14 is also a part of the type specimen.

Type locality: Stuttgart-Heslach (Fig. 1.1). The exact locality is unknown, but the specimen comes most probably from the "Heslacher Wand". For details, see Appendix C, 4.1.

Type horizon: lower or middle Stubensandstein (see discussion in Appendix C, 4.2).

Paralectotype: SMNS 54708: anterior half of a left premaxilla (PLIENINGER 1857: pl. 8 fig. 1; MEYER 1861: pl. 31 figs 9-12; Fig. 2.4). According to KURR (1852), the specimens comes from Affaltrach near Löwenstein (Fig. 1.1), but exact locality details are not available (see Appendix C, 1.1.2 and 1.2).

Referred specimens: If not stated otherwise, the material is part of the former KAPFF collection, which is exclusively derived from unspecified quarries around Heslach and Kaltental. An overview of the cranial material is given in Figure 2.1.

(1) Skulls and skull fragments:

SMNS 4378: skull lacking the right temporal region, the posterior part of the left squamosal, and most of the ventral processes of the pterygoids (MEYER 1863: pls. 38-40, pl. 42 figs. 1-5; Fig. 2.5 - 2.7, Fig. 2.44A-B). The posterior part of the braincase is exposed. The skull was recently restored, but the squamosals are too long and were fitted with pointed posterior processes and undifferentiated paroccipital processes, in addition, the squamosal processes of the parietals are very high, and the ventral processes of the pterygoids too large and too steep in comparison with the other skulls. For measurements, see Table 2.2.1.

SMNS 4379: a complete and almost undistorted skull, but with poorly preserved sutures on the dorsal surface (FRAAS 1896: pl. 5 fig. 1; Figs. 2.8 - 2.11). A lower jaw recovered nearby and referred to the same specimen (MEYER 1863: 227) is not preserved in the collection. The occipital aspect is only partially prepared. For measurements, see Table 2.2.1. A cast of this skull was widely distributed by the fossil merchants Krantz (e.g. Long & Murry 1995: figs. 40C, 56A-B).

SMNS 5725: preorbital part of a large skull with exceptionally well preserved sutures on the dorsal surface in contrast to the palate, which has suffered from intensive fragmentation (HUENE 1911: fig. 13; Figs. 2.12 - 2.14, Fig. 2.43B). For measurements, see Table 2.2.1.

SMNS 5726: complete skull though somewhat obliquely distorted, showing well preserved sutures (ZITTEL 1923: fig. 561; HUENE 1911: figs. 12, 14 - 15; Figs. 2.15 - 2.17, Fig. 2.43A). Details of the occipital aspect are largely obscured by coatings of hematitic crusts. All teeth are restored. For measurements, see Table 2.2.1.

SMNS 5727: skull completely freed of matrix, showing the snout and left postorbital portion of skull undeformed (Figs. 2.18 - 2.20, Fig. 2.27, Fig. 2.44D-F). Large parts of the right postorbital side, the orbito-nasal region, the posterior palatal region and the anterior left premaxilla are restored in resin. Almost no sutures are

Table 2.2.1 *Nicrosaurus kapffi*, cranial measurements

All measurements are in mm. The specimens are ordered in accordance with skull length. The numbers 1 - 24 correspond to the distances illustrated in Figure 2.2.

character	BMNH 42743	SMNS 4379	SMNS 4378	SMNS 5727	SMNS 5726	SMNS 4060	SMNS 13078	SMNS 5725	BMNH 38043
1 skull length overall	730 (est.)[1]	730	750	765	775	790 (est.)[2]	900 (est.)[2]	920 (est.)[1]	indet.
2 distance tip of snout - basioccipital condyle	655	660	676	680	690	indet.	indet.	indet.	indet.
3 distance tip of snout - anterior corner of antorbital fenestra	415	412	415	401	420	indet.	indet.	450	indet.
4 distance tip of snout - anterior corner of naris	405	430	408	399	435	indet.	indet.	450	indet.
5 distance tip of snout - anterior rim of orbit	530	535	529	537	560	indet.	indet.	600	indet.
6 distance tip of snout - anterior corner of infratemporal fenestra	525	540	529	541 / 519	545	indet.	indet.	600	indet.
7 distance between orbit and naris	77	77	74	88	66	indet.	indet.	82	indet.
8 maximum width quadrate - quadrate	298	308	(275)	320	320	indet.	indet.	indet.	indet.
9 maximum width squamosal - squamosal	(115)	233	indet.	204	211	indet.	indet.	indet.	indet.
10 height quadrate - skull roof	130	115	130	110	130	indet.	indet.	indet.	indet.
11 width of snout at anterior constriction	34.3	47	44.5	54	46	35	56	70	indet.
12 width of snout at posterior constriction	42.6	62	55.6	66.6	59	58	68.6	115	indet.
13 width of skull roof	121	134	140	130	152	indet.	indet.	indet.	indet.
14 width of postorbito-squamosal bar	30.1 (s)	36.5 / 40	28	37	34 / 34	indet.	indet.	indet.	28.8[3]
15 length of postorbito-squamosal bar	indet.	123	indet.	140	135 / 126	indet.	indet.	indet.	indet.
16 length of squamosal (min - max)	indet.	indet. -95	indet.	indet.	65-98 (s)	indet.	indet.	indet.	82-100

Table 2.2.1 (continued)

17 length of posterior process of squamosal	indet.	35	indet.	31	indet.	indet.	indet.	indet.	32.2[4]
18 axial diameter of orbit	53.7 (d)	58.2 / 61.3	66.5 / 64.6	57 / 54.8	61 (d)	indet.	indet.	indet.	indet.
19 transverse diameter of orbit	43.8 (d)	38.8 / 37.4	36.5 / 46	indet.	34 (d)	indet.	indet.	indet.	indet.
20 width of supratemporal fenestra (anterior rim)	18.2 (d)	16 / 15.5	21 (s)	24.1 / 20	17.5 (s)	indet.	indet.	indet.	indet.
21 width of supratemporal fenestra at quadrate	indet.	64	indet.	84.4	72	indet.	indet.	indet.	indet.
22 width of supratemporal fenestra at tip of squamosal	indet.	200	indet.	217	215	indet.	indet.	indet.	indet.
23 width of posttemporal fenestra	indet.	indet.	28.5	19	indet.	indet.	indet.	indet.	indet.
24 height of posttemporal fenestra	indet.	indet.	13.5	6	indet.	indet.	indet.	indet.	indet.
length of parietal foramen	–	–	–	14	10	indet.	indet.	indet.	indet.
thickness of postorbito-squamosal bar at anterior corner of infratemporal fenestra	18	indet.	indet.	18	(17)	indet.	indet.	indet.	(13.4)[5]
depth of palatal vault	39	24	30	63	24	indet.	indet.	indet.	indet.

[1] estimated according to preorbital length

[2] estimated according to the length of the premaxilla

[3] for preservational reasons, maximal width of the squamosal

[4] for preservational reasons, the distance between the tip of the squamosal and the paroccipital process of the squamosal (i.e. a somewhat greater figure)

[5] for preservational reasons, maximal thickness of the squamosal

Symbols and abbreviations:

( ) = minimal value given because of incomplete preservation or limited accessibility; – = not present in specimen; / = left side / right side; (d) = dexter, right; (est.) = estimated; indet. = indeterminable because of incomplete preservation; (s) = sinister, left.

traceable, and the braincase is very poorly preserved, but a remarkably complete dentition is present. For measurements, see Table 2.2.1.

SMNS 13078: prenarial portion of a snout of a large individual with well-preserved dentition (Fig. 2.27). For measurements, see Table 2.2.1. Collected from a former sand quarry at Abelsberger Straße, Stuttgart-Gaisburg (Fig. 1.1).

SMNS 54706: isolated right temporal and cheek region (MEYER 1861: pl. 32 figs. 1-2, pl. 35 fig. 1; Fig. 2.21). The jugal and the parietal were detached before burial along the sutures with the maxilla, lacrimal and ectopterygoid, and the left parietal, respectively. The body and the posterior process of the squamosal are pressed in a vertical plane. Most of the parieto-squamosal bar is missing, the squamosal process of the parietal is pressed towards the postorbito-squamosal bar; consequently the width of the supratemporal fenestra is significantly reduced. The incomplete paroccipital process is detached from the squamosal and rotated ventrally.

BMNH 42743: skull lacking most of the posterior parts behind the supratemporal fenestrae. The snout is intensely fractured in front of the nares, and the prenarial area just behind the slope of the crest is crushed down (Figs. 2.22 - 2.25, Fig. 2.44C). For measurements, see Table 2.2.1. Ex KAPFF collection, purchased in 1867 as part of the VAN BREDA collection (LYDEKKER 1888).

SMNS 56989: longitudinally split snout fragment, largely unprepared. Sindelfingen-Magstadt (Fig. 1.1)

BMNH 38043: dorsoventrally compressed left squamosal.

SMNS uncat. no. 12: ventral part of a quadrate lacking most of the craniomandibular joint surface, with very thick jugal-quadratojugal bar. The specimen was described briefly in MEYER (1861: 284).

GPIT 2223.000: fragment of the posteroventral parts of both premaxillae, including the base of the prenarial crest. History unknown, but according to the specimen label, this specimen is from Stuttgart-Degerloch.

(2) Mandibles:

SMNS 4380: complete, articulated mandible with poorly preserved dentition (MEYER 1861: pls. 46-47), according to MEYER (1863: 227) found in the vicinity of the skull SMNS 4378 and probably belonging to it. During restoration in 1985, the tip of the mandible and much of the bone surface was covered with resin. All teeth were extracted, cleaned, partly or fully restored, and reset in the jaws (O. MAASS, SMNS, pers. comm., 1994). For measurements, see Table 2.2.2.

SMNS 5730: complete right mandibular ramus with 16 teeth, five of which are artificial. For measurements, see Table 2.2.2.

SMNS uncat. no. 9: posterior part of a right mandibular ramus (MEYER 1861: pl. 34 figs. 1-4).

BMNH 38036: complete, articulated mandible with a total of 64 teeth preserved. For measurements, see Table 2.2.2.

BMNH 42744: complete, articulated mandible with a total of 19 teeth preserved. For measurements, see Table 2.2.2.

GPIT uncat. no. 399: fragment of left mandibular ramus at the end of the symphysis, including one tooth. Heslach (specimen label). History unknown.

Table 2.2.2 *Nicrosaurus kapffi*, mandible measurements (in mm).

	SMNS 4380	SMNS 5730	BMNH 38036	BMNH 42744
total length	717	747	715	710
length of symphysis (% of total length)	297 (41.5%)	320 (43%)	280 (39%)	290 (41%)

(3) Postcrania: None.

Summary description: Large (skull 730 to >900 mm in length) and robustly built species of *Nicrosaurus*; well marked ventral expansion of the posterior alveolar rim of the premaxillary; maxilla usually distinctly flared; septomaxilla extends far beyond the anterior tip of the nasal, and may terminate in several prongs; narial rim undulating without narial wing; postorbito-squamosal bar more slender and thicker (c. 20 mm) than in *Nicrosaurus* species B; supratemporal fenestra cuts deeper into the skull roof than in *Nicrosaurus* species B, and is consistently wide and always rounded anteriorly; dorsal rim of the squamosal process of the parietal steep and less overhanging the supraoccipital shelf; supraoccipital shelf short anteroposteriorly; a fossa on the parietals communicates between the skull roof and the supraoccipital shelf; body of the squamosal low compared to *Nicrosaurus* species B; squamosal contacts the anterior and probably the posterior face of the paroccipital process; quadratojugal process of the squamosal extends along, at most, half of the infratemporal fenestra; in dorsal view, the posterior process of the squamosal is continuously broad, with a thickened medial rim, and the process terminates in a rounded rim, with posteromedially facing flat surface and ventrally pointing blunt knob; the paroccipital process of the squamosal is large; posttemporal fenestra bound laterally by a stout process of the squamosal that lies on the paroccipital process; base of the paroccipital process comparatively less wide, and cylindrical with a weak posterior ridge; the lateral part is broad anteroposteriorly with a shelf in front of the opisthotic ridge

and a vertical posterior face; ridges of the stapedial and the jugular groove low and sharp-edged; prechoanal vomers always of rhombic shape; ventral edge of the quadratojugal-jugal bar usually round; well developed grooves on the pterygo-quadratal bar; craniomandibular joint of the quadrate massive and wide, the lateral condyle largely confluent with the cheek; inclined anteroventral face of the quadrate with prominent muscle scars; basipterygoid processes stout and less splayed than in *Nicrosaurus* species B; basal tubera less wide transversely and face posteroventrally; upper jaw dentition with three sets of teeth (tripartite dentition, see subsection 2.2.4); symphysis equals c. 40% of the total length of the mandible.

Diagnosis: continuous prenarial crest from the external nasal openings to the end of the downturned tip of snout; prenarial crest straight or convex at about the level of the skull roof.

Distribution: in central Württemberg Heslach, Kaltental, Gaisburg, Backnang, and (probably) Degerloch, all villages on the periphery of Stuttgart, and Sindelfingen; in northern Württemberg Affaltrach near Löwenstein (Fig. 1.1).

Stratigraphic range: Upper Triassic, Keuper succession, Middle Keuper, Stubensandstein, middle Stubensandstein, based on SMNS 13078 and SMNS 56989 (see Appendix C, 5 and 7). The occurrence of *Nicrosaurus kapffi* in the lower Stubensandstein, which was postulated by WILD (1991) and BENTON & WILD (1993), cannot be assessed on the base of the data preserved and has to be confirmed by new finds (see discussion in Appendix C, 4.2).

Age: Early (to Middle?) Norian, Late Triassic.

2.2.3 The cranium of *Nicrosaurus kapffi*

2.2.3.1 The shape and the sculpture of the cranium

The shape of a phytosaur skull is an important part of its anatomy for comparative and phylogenetic purposes. Since the configuration of the skull elements in many specimens, among them type specimens like these of *Rutiodon carolinensis* and *Arribasaurus buceros*, is rather imperfectly preserved, a good number of descriptions deal more with the general appearance of the skull rather than with osteological details (COPE 1881; EATON 1965; HELLER 1954; HUENE 1915a; HUNT & LUCAS 1993c; LONG & MURRY 1995). Perhaps as a consequence of this, phylogenetic investigations have mostly focused on characters of the general skull morphology rather than on osteological details. For this reason, I give a separate account of the general skull morphology of *Nicrosaurus kapffi*. In a strict sense, the description applies to the robust morph only; differences found in the gracile morph are pointed out and discussed under the heading of variation (2.2.7). A number of phylogenetically important characters, which include structures formed by several bones (see BALLEW 1989) and which are therefore difficult to address in the structure of an osteological description, are included here.

Snout: The tip of the snout in *Nicrosaurus kapffi* is turned downwards and expanded laterally to form a spoon-shaped extension. For this reason, an anterior constriction of the rostrum is developed at the narrowest point of the snout (Figs. 2.16, 2.23). The degree of the ventral deflection varies individually, ranging from a moderate bent with the tip of the snout terminating roughly at level with the alveolar rim (e.g. Figs. 2.3AB, 2.14, 2.20) to a steeply downturned terminal rosette, in which the alveoli of the anteriormost two premaxilla teeth are well set beyond the level of the post-tip dentition (Figs. 2.4, 2.24). Along the premaxillae backward, the snout remains comparatively narrow until the jaws expand abruptly to receive the enlarged posterior premaxillary teeth. This results both in a depression of the alveolar border of the premaxilla (Figs. 2.15, 2.18) and a posterior constriction at the level of the premaxilla-maxilla suture (Figs. 2.12, 2.16, 2.20), which is at about mid-length of the snout (pre-constrictional length varies between 47 and 54% of total snout length). In the posterior third, the width of the snout increases significantly by means of the widely arched posterior parts of the maxillaries. Here, the maxillaries are distinctly flared, and in dorsal view they form a shelf-like, dorsolaterally to dorsally facing expansion of the snout (Figs. 2.8, 2.12, 2.15, 2.18). The alveolar border of the maxilla is slightly concave as well (Figs. 2.10, 2.14, 2.20, 2.24), but never reaches such a degree of concavity as can be found in some other

phytosaurs with massively built snouts (compare with specimens of *Paleorhinus sawini*, *Leptosuchus* spp. or *Smilosuchus gregorii* in LONG & MURRY 1995: figs. 24A, 28, 29B). As a consequence, in *Nicrosaurus kapffi* the ventral emargination of the jugal just below the orbit is less well developed than in these species.

Prenarial crest: The prenarial crest, the most conspicuous feature of *Nicrosaurus kapffi*, extends in all specimens from the narial openings to the beginning of the downturned tip of the snout. Over a distance of about 100 mm just in front of the nares, the posteriormost part is laterally constricted to the narrowest point of the prenarial crest as a result of the bulging narial bulb (e.g. Figs. 2.8, 2.15). Here, the apex is hemicircular and the flanks of the crest are somewhat concave. Unlike all other crested phytosaurs, the prenarial crest of *Nicrosaurus kapffi* does not slope down gradually in an anterior direction from the naris or from a distinct point on the snout, but the top is straight or even convex in outline (see variation, subsection 2.2.7). Along the snout, the highest point of the crest reaches the level of the skull roof at best, but is usually well below this. The prenarial crest is never developed as a sharp knife-like edge as in e. g. *Arribasaurus buceros* or some individuals of *Nicrosaurus* species B, but is always rounded or even flat-topped (Fig. 2.12). Despite the frequent *post-mortem* deformations, it is obvious, in dorsal view, that the crest follows a slightly mediolaterally undulating course (Figs. 2.5A, 2.8, 2.22). The crest ends abruptly in a steep and rounded slope.

Internal structure of the prenarial crest: In the lectotype SMNS 4060, the anteriormost part of the rostrum including the terminal rosette has been separated from the snout along an oblique old fracture, at about the level of the 8th premaxilla tooth. The cross-section of the anterior fragment (Fig. 2.3D) reveals a remarkable insight into the internal structure of the prenarial crest of *Nicrosaurus kapffi*. The crest is not a massive bony structure, but hollowed by large cavities, which might correspond to the premaxillary or tubular cavity anterior to the antorbital cavity in numerous phytosaurs (*Rutiodon carolinensis*, *Smilosuchus gregorii* [WITMER 1997: fig. 22A-C], *Pseudopalatus pristinus* [CAMP 1930: fig. 24b-c], *Arribasuchus buceros*, *Mystriosuchus planirostris* [WITMER 1997: 48], and *Nicrosaurus* species B [pers. obs., BMNH 38039]. In contrast to these taxa, however, the cavitas in the anterior part of the snout of *Nicrosaurus kapffi* is separated into two cavities by a thin, vertical lamella along the mid-line of the rostrum, which represents the contact between both premaxillae. The undulating trace of the septum in Figure 2.3D is corroborated by the right snout fragment SMNS 54708, in which the interpremaxillary suture shows a similar, irregularly corrugated, but smooth surface in medial aspect. More importantly, each cavity is further subdivided by a system of waver-thin internal lamellae and struts, which project interiorly

from the internal lateral and ventral surface of the premaxilla. The internal lamellae form a multifurcated, complex three-dimensional mesh, and it is visible in some parts of the cross-section that they enclose smaller caverns within the prenarial crest cavity. However, because of poor preservation and crushing it remains unclear how far these lamellae extend into the centre of the crest cavity, nor can be established from the position of the section whether the prenarial crest cavities communicate with the antorbital cavity. Further intrusive examination or computerised tomography are needed to clarify the detailed structure of the prenarial crest cavities and to create a sound basis for a functional interpretation.

Narial region: The nasal openings are about level with the prenarial crest, as well as with the skull roof. The anterior narial edge is confluent with the crest, however, the septomaxillaries form a low but distinctive hump just in front of the nares. In detail, the outline of the lateral rim of the naris is undulating, but it is never drawn out to a distinct narial wing as in some specimens of *Nicrosaurus* species B or in *Mystriosuchus*. The posterior edge of the narial rim appears somewhat elevated, but this is mainly a result of the saddle-shaped area between the nares and the orbits. The internarial septum is thick and at level or even slightly depressed relative to the narial rim. The flanks of the snout below the nares are convex. This is much more pronounced by the presence of a longitudinal recess, here introduced as infranasal recess, at the base of the flank of the narial region immediately dorsal to the antorbital fenestra (Figs. 2.5C, 2.10, 2.14, 2.20). The infranasal recess shows a somewhat ragged and irregular outline (Figs. 2.10, 2.14). Since the prenarial crests in all specimens have been deformed by post-depositional compaction and are usually inclined to one side, the recess is more pronounced on the side that suffered compressional deformation (e.g. Fig. 2.8). The presence of an infranasal recess and the convex flanks of the snout in that area leads to the bulbous, laterally expanded appearance of the narial region, here called the narial bulb. The infranasal recess continues anteriorly for a distance, and distinguishes the posterior part of the crest from the flaring maxillar portion of the snout.

Interorbitonasal region: The posterior snout profile is slightly concave because of a gentle rise to the nares anteriorly and a more pronounced ascent to the orbits posteriorly, depending on the height of the postorbital skull. The top of the snout broadens consistently here, and the rounded, sloping flanks lead to a saddle-shaped interorbitonasal region (Figs. 2.10, 2.20).

Postorbital part of the skull: Following the constriction by the jugal notch, the cheek of *Nicrosaurus kapffi* bulges strongly outwards. This results in the broad and

massive general appearance of the skull. The plane of the skull roof itself broadens only gently, but steadily, essentially by means of the somewhat outward turned and straight postorbito-squamosal bar and the dorsal surface of the squamosal aligned to it. The postorbito-squamosal bar is thin, and shows a consistent, comparatively large width over the whole length.

Palate: The alveolar ridges (the "anterior palatal ridge" of CAMP 1930) on the premaxilla and maxilla appear to be more massive, but are not as prominent as in *Nicrosaurus* species B. As is common in phytosaurs, the palate is subdivided in two parts (Figs. 2.9, 2.11). There is the essentially flat palatal plane on the level of the ventral snout surface, which includes the maxilla and the horizontal parts of the palatine and the ectopterygoid surrounding the suborbital fenestra. The palatal vault is a centrally placed dome around and behind the choanae, which is formed by the vomers, the medial wings of the palatines, and the pterygoids.

Sculpture: MEYER (1863: 237-238) dedicated two pages to describing the sculpture of the crest and skull roof in SMNS 4378 in remarkable detail. The different superficial features he observed can be found in the other skulls as well, and his observations are completed and discussed here.

The top of the crest. Unlike the skull roof and flanks of the snout, the rounded top of the prenarial crest usually shows no regular distributed and prominent sculpture over most of its length, except perhaps some minor rugosities (Figs. 2.8, 2.18, 2.22). However, in the overall majority of skulls there are deep, irregularly spaced and shaped pits or holes, which in all cases are confined to the anterior half of the crest (Figs. 2.5A, 2.12, 2.18). Some areas of the crest top might even be raised by conspicuous bony outgrowths (SMNS 5726: Fig. 2.15). The presence of these excavations form the basis of ABEL's (1923) hypothesis that the structures (and the whole prenarial crest) in *Nicrosaurus kapffi* are pathologic lesions following injuries sustained in intraspecific combat. It has also been suggested that these structures indicate the presence of a display structure on the snout that had no potential of being fossilised, for example a sheath of horn topping the prenarial crest (ZIEGLER 1986, HUNGERBÜHLER 1995). However, in two skulls (SMNS 4379: Fig. 2.8; BMNH 42743: Fig. 2.22), the crest tops are essentially smooth. There is no indication at all for foramina (vessels) which must be postulated to provide nutrients to a soft tissue structure. In the area of the pits, the bone tissue seems to have been extensively remodelled, which regularly affects the straight course of the interpremaxillary suture so that it undulates or is even obscured. Having examined all skulls, I think now that there is too much contradictory evidence to postulate the presence of any soft tissue display structure. It is more plausible to interpret these

observations in terms of secondary phenomena (pathologies or ontogenetically controlled bone alterations) than normally present surface sculpturing. The identification of a traumatic nature must await histological studies (cf. MOODIE 1922).

The flanks of the crest. The flanks of the prenarial crest are, in some specimens, sculptured with vertical, broad and shallow ridges resulting in a slightly undulating lateral surface of the crest (Fig. 2.5C, 2.24). All flanks are composed from several lamellar layers of bone which apparently grew successively from the base towards the top of the crest. The dorsal and lateral extent of each lamella varies according to the timing of their formation, the more profound the lamella the larger is its spread over the crest flank. This results in an array of ridges, the indented and rounded dorsal edges of individual lamellae, which are crossing obliquely the flanks of the crest (Figs. 2.10, 2.15).

The foramina of the snout. There is an array of foramina, probably for nerves and blood vessels supplying the skin, running parallel to and in about 20 mm distance above the alveolar margin (Figs. 2.5C, 2.10, 2.14, 2.24). Especially in the middle section of the snout, the openings are confluent and form a distinct groove along the jaw line. In the posterior two thirds of the maxilla, the groove is not continuous, but frequently interrupted, and especially towards the extremity of the jaw the groove is broken up into a linear array of larger pits. Numerous single foramina are concentrated on the dorsal surface of the expanded tip of the snout (Figs. 2.5A, 2.15, 2.24). It has been suggested that such foramina may have housed receptors for a sensory (tactile) organ (CAMP 1930), but there is no additional evidence for the hypothesis.

Dermal bones of the skull roof. The common sculpture of the skull is a mosaic of elongated pits which are separated by broad and blunt ridges. The ridges are the more conspicuous component of the sculpture. The pits are shallow, but usually well defined. This type of sculpturing is well developed in the interorbitonasal region and on the skull roof, to a lesser degree on the postorbito-squamosal bar and the posterior process of the squamosal as well.

In two areas of the dorsal skull surface, the ridge-and-pit sculpture is substituted by another type of surface ornamentation: these are the infranasal recess between the narial bulb and antorbital fenestra on the nasal and the maxilla, which continues forward horizontally on the premaxilla, and a broad area on the lacrimal connecting the orbit and the antorbital fenestra (Figs. 2.5A, 2.5C, 2.10, 2.14, 2.18). Both these areas, especially the infranasal recess, are conspicuously sculptured with an array of parallel, short ridges that are directed posteromedially and thus separate deep and smooth grooves. The sculpture is difficult to explain in terms of functional significance. The ridges could indicate a spreading of muscle fibres or tendons out of the antorbital fenestra on the dorsal surface of the skull. However, the orientation of the ridges is exactly opposite to

the reconstructed orientation of muscle fibres of the M. pterygoideus anterior (ANDERSON 1936).

Circular holes. The nature of some peculiar structures on three of the skulls is unclear. Four oval holes (8 x 5.5 mm) are arranged in a square on the right dorsal face of the snout SMNS 4060 (Fig. 2.3D). The holes are still infilled with matrix which precludes an explanation as preparatorial damage. A more cylindrical hole (diameter of 6 mm) penetrates deeply the dorsal surface of the squamosal in SMNS 54706 (MEYER 1861: pl. 32 fig. 1), and a shallow oval depression (7.5 x 5 mm) is present on the lateral side of the left squamosal of SMNS 5727. In all cases the shapes of the holes are very regularly oval-shaped, the penetration may be extremely deep despite the rather small diameter and the massive cortical bone tissue, and there is no evidence of concentric or radiating microfractures nor bite mark furrows on the surrounding bone surface. The holes therefore hardly correspond to the characters of punctures attributable to tooth marks of a predator (see CRUICKSHANK 1986, ERICKSON & OLSON 1996, FIORILLO 1991, HAYNES 1980 for morphology of tooth marks in bones). Bones penetrated by borings are rare in the fossil record (ROBERTS & ROGERS 1997; ROGERS 1992 and references therein). Although HUNT et al. (1993) report the presence of round to ovoid invertebrate borings in a phytosaur skull, I think the evidence is still too insufficient to attribute the holes in *Nicrosaurus*-skulls to the post-depositional activity of boring organisms.

2.2.3.2 The openings of the cranium

External naris: The naris is bound by the nasal posteriorly and laterally. The septomaxilla borders the naris in front and contributes much to the internarial septum. The shape of the naris is elongated anteroposteriorly with the anterior end being slightly more pointed. Both ends tend to be splayed outwards which leads to a kidney-shaped opening. The rim of the nares is undulating, and there is no narial wing nor an anterior groove developed.

Antorbital fenestra: The antorbital fenestra is an elongated, oval-shaped opening below the nares. It is typically three times as long as wide, but frequently the width is drastically reduced on one side by post-mortem deformation of the skull (e.g. SMNS 4379, left side: Fig. 2.8; SMNS 5726, right side: Fig. 2.15). In lateral view, the antorbital fenestra is somewhat inclined anterodorsally. It opens in dorsolateral direction (but see variation, subsection 2.2.7).

The antorbital fenestra is surrounded by the dorsal and ventral processes of the maxilla, the lacrimal, and the jugal. In some specimens, however, the jugal is excluded

from participating by a broad maxillo-lacrimal bar. The nasal may contribute to the dorsal margin of the antorbital fenestra as well (see variation, subsection 2.2.7).

Orbit: The orbit is oval-shaped. A more or less prominent protuberance of the orbital rim in the anterodorsal corner accounts for a somewhat irregular outline. The dorsal orbital rim is formed by prefrontal, frontal, and postfrontal. The lacrimal borders the orbit anteriorly, the postorbital posteriorly and posteroventrally (Fig. 2.40). The jugal is usually excluded from the orbit, but may interrupt the postorbito-lacrimal bar to participate at the ventral rim (see variation, subsection 2.2.7; Fig. 2.43). The orientation of the orbits varies in correlation with the skull height (see variation, subsection 2.2.7; Fig. 2.44A, D).

Supratemporal fenestra: The anterior third of the supratemporal fenestra is emarginated in the skull roof. The straight anterior and medial border is formed by the parietal, the postorbital contributing only for some distance in the anterolateral corner. The parieto-squamosal bar consists of the thin ridge-like squamosal process of the parietal, running steeply downward and outward to meets the horizontal anteromedially directed parietal process of the squamosal (Fig. 2.40). Hence, the posterior border of the supratemporal fenestra is oriented obliquely to the skull axis (Fig. 2.39) and is depressed below the level of the skull roof, the dorsal surface of the bar being lowered for an amount of 20 to 25% of the total skull height. The lateral border formed by the postorbital, the body and the postorbital process of the squamosal is straight, which accounts for the subrectilinear outline of the supratemporal fenestra in the skull roof (Fig. 2.39). Since the postorbito-squamosal bar overhangs the lateral part of the fenestra, the width visible in dorsal view is reduced to about one half of the actual size as defined by the posterolateral extent of the parieto-squamosal bar.

Infratemporal fenestra: The infratemporal fenestra is of rhomboidal outline, the posteroventral corner being not acute but more of a gently rounded appearance. The opening is higher than wide and the long axis of the fenestra is directed posterodorsally. The anteriormost anteroventral corner lies directly under the anterior rim of the orbit. The inclination of the infratemporal fenestra to a sagittal plane depends on the height of the skull and is therefore discussed under the heading of variation (subsection 2.2.7). The fenestra is surrounded by the posterior and postorbital processes of the jugal, the postorbital, the postorbital and quadratojugal processes of the squamosal, and the quadratojugal (Fig. 2.40).

Parietal foramen: SMNS 5726 and SMNS 5727 show a conspicuous excavation on the posterior skull roof (Figs. 2.15, 2.18) which is absent in all other skulls. In both specimens, the pits are elongated anteroposteriorly and situated in the same position on the interparietal suture close to the contact with the frontals. Moreover, in SMNS 54706 the surface of the right interparietal joint is exposed. A broad canal can be seen running from the brain cavity backwards and upwards and terminating in an oval cavity just beneath the dorsal surface of the parietal (Fig. 2.21B). The concavity corresponds in size and position to the "dome-like excavation" in the parietals described by CAMP (1930: 94, fig. 25) in *Smilosuchus gregorii*. Both these structures resemble a secondarily closed epiphyseal canal leading from the parietal surface to the brain, and thus the pits in SMNS 5726 and 5727 represent most likely a persisting parietal foramen. However, the interpretation remains somewhat ambiguous by the fact that the other skulls lack such an opening and similar pits can be present within bones on the skull roof as in SMNS 5726 (one close nearby in the interfrontal suture and another within the right frontal, Fig. 2.15) and in BMNH 42743 (at the triple junction of postorbital, postfrontal and parietal, Fig. 2.22). Another difference from a juvenile specimen with a clearly persisting parietal foramen mentioned by CAMP (1930) is that the pits in the two skulls of *Nicrosaurus kapffi* do not lie in an elevated portion of the parietals, nor is there any trace of such an elevation in the skulls lacking the foramen (in contrast to *Mystriosuchus* species B; HUENE 1911).

Posttemporal fenestra: The posttemporal fenestra is large (in comparison to *Pseudopalatus* and *Mystriosuchus*) and situated below the medial half of the supratemporal fenestra (Figs. 2.6, 2.41). The descending squamosal process of the parietal and the parietal process of the squamosal arch over the posttemporal fenestra. For preservational reasons, the configuration of the bones surrounding the fenestra cannot not be resolved satisfactorily, and was reconstructed in Figure 2.41 using information from *Nicrosaurus* species B (Fig. 2.58). While the parietal process of the squamosal clearly forms the dorsolateral border, it remains unsolved, whether and over how long a distance the parietal and the supraoccipital participate in bordering the posttemporal fenestra. The supraoccipital touches at least the medial corner of the fenestra where it meets the opisthotic, but the length of its contribution is unclear since the exact length of the parietal process of the squamosal cannot be established (SMNS 4378: Fig. 2.6). The configuration in SMNS 5726 might suggest that the parietal is excluded from the opening as in *Nicrosaurus* species B (Fig. 2.58) and *Mystriosuchus* species B (Fig. 3.5). The base of the paroccipital part of the opisthotic forms the rounded medioventral rim of the opening. Because of the dorsoventral expansion of this process, the fenestra tapers continually toward the lateral side. According to SMNS 4378, an medioventral extension

of the parietal process (= opisthotic lamella) of the squamosal extends on the paroccipital process and thus borders the posttemporal fenestra ventrolaterally (Fig. 2.6).

Foramen quadrati: The foramen quadrati is situated in the upper part of the suture of the quadrate and quadratojugal, at about the level of the tip of the paroccipital process of the squamosal (Fig. 2.41). It lies in a deep vertical recess surrounded by both bones and is thus visible only in posterior view. The actual opening is teardrop-shaped, with the tip pointing ventrally. From the tip, the ventral part of the recess leads downward as a groove along the quadrate-quadratojugal suture and disappears above the lateral condyle of the quadrate. In some specimens, a second shallower groove can be seen trailing ventromedially on the occipital surface of the quadrate from the quadrate foramen to the medial condyle.

Pteroccipital fenestra (cranio-quadrate passage): The pteroccipital fenestra is a passageway leading from the ventral occipital area between the pterygo-quadrate plate and the paroccipital process along the braincase into the adductor chamber. It is a narrow, fissure-like opening and, according to the course of the bordering skull structures, oriented anteromedially (Figs. 2.5B, 2.11). The ventral border is formed by the dorsal rim of the pterygo-quadrate plate, i. e. from front to back, the squamosal wing of the pterygoid and the pterygoid wings of the quadrate (Fig. 2.25) and the squamosal (Fig. 2.7), respectively. The paroccipital process arches over the pteroccipital fenestra dorsolaterally. Dorsomedially, the fenestra is outlined by the ventrolateral edge of the braincase in front of the tuber basioccipitalis, where it terminates above the basipterygoid joint.

Choana: The choana illustrated in Figure 2.9 lies in the anterior part of the palatal vault and is thus raised compared to the lateral and anterolateral parts of the palate. The exact position of the choana relative to the naris varies but insignificantly: in most of the specimens the anterior rim is placed exactly below the anterior rim of the external nares, but it can be slightly (less than 10 mm) shifted in front (see variation, subsection 2.2.7). The choana is, however, more elongated posteriorly reaching about 1.5 times the length of the naris. The opening is of subrectangular shape.

The choana is bordered anteriorly by a medial process of the maxilla. There is no clear evidence that the premaxilla reaches the choana. The lateral border is formed by a vertical lamella of the palatine and in its posterior part overhung by the palatal ridge. A lateral extension of the vomer marks the posterior rim of the choana.

The interchoanal septum is exclusively formed by the vomers. It is slightly constricted in its middle part. There is an elongated and prominent ridge in mid-line of the

septum just at the anterior tip of the choana, which brings the ventral edge of the interchoanal septum at the lower level of the palatines. At about the middle of the choanae, the septum curves steeply upward to reach in its posterior part the deeper level of the palatal vault (Fig. 2.16).

Interpterygoid vacuity: Since the pterygoids meet along the midline over most of their length, the interpterygoid vacuity is a vestigial opening just in front of the basisphenoid (Figs. 2.5B, 2.16). The basipterygoid joints form the lateral border (Fig. 2.25). The posterior part of the cultriform process of the parasphenoid separates the vacuity into two drop-shaped holes, which both together indentate the palatal vault (Figs. 2.9, 2.19).

Suborbital fenestra: The suborbital fenestrae are about twice as long as figured in MEYER's (1863: pl. 39; Fig. 2.5B) somewhat idealised ventral aspect of the SMNS 4378. In reality, they are much more elongated and narrower openings situated between the palatine and the ectopterygoid (Figs. 2.9, 2.16, 2.19, 2.23). Also in contrast to MEYER's figure, the maxilla contributes to the anterior rim in all specimens. The long axis of the slit-like fenestra is orientated anterolaterally, but the slit is somewhat curved to the lateral side resulting in a convexity of the opening towards the medial side. The anterior and posterior ends are in most of the specimens slightly expanded and thus of a bulbous appearance. The exact shape of the suborbital fenestra is probably subject to ontogenetic variation (see variation, subsection 2.2.7).

Subtemporal fenestra: The large subtemporal fenestra housing mainly the Mm. adductores mandibulae is approximately triangular, with a broadly rounded apex pointing posteriorly. The opening is bound by the broad pterygo-quadrate bar posteromedially and the elongated glenoid facet of the quadrate posteriorly. The lateral convex bar is formed by the quadratojugal and the jugal. The ectopterygoid and the basal ectopterygoid wing of the pterygoid limit the subtemporal fenestra anteromedially.

The posterior wall of the subtemporal fenestra is characterised by at least four large muscle scars which are situated on the ventral part of the internal surface of the quadrate and its pterygoid wing, medial and ventral to the inlet of the foramen quadrati (Fig. 2.19). These parts of the bone are inclined anteriorly in contrast to the vertical upper part of the quadrate, thus forming a broad concave internal surface. The scars are delineated by prominent ridges, which travel obliquely upward and inward, and lead to the presence of elongated shelves or sinuses as attachment points of jaw muscles.

2.2.3.3 Osteology of the cranium

Although *Nicrosaurus kapffi* is represented by five almost complete skulls, no or only little morphological data is available about the bones in the anterior part of the braincase. In SMNS 5727, the whole braincase is present and mostly freed from adherent matrix (Figs. 2.20), but because of the overall poor preservation of the specimen the neurocranial structures are largely indeterminable and no sutural connections of the individual elements can be traced. In the other specimens, the internal aspects of the temporal, occipital, and palatal regions are still obscured by matrix. An exception is SMNS 4378, in which at least the posterior part of the braincase is almost perfectly exposed (Fig. 2.7). In no specimen are the most delicate bones of the neurocranium and the otic region preserved. For this reason, the stapes, the epipterygoid, the presphenoid, the laterosphenoid and the prootic are not included in the description.

Median dorsal skull elements:

Premaxilla. The premaxillaries are massive bones that form the anterior two thirds of the rostrum. On the top of the prenarial crest, each bone shows a narrow and short dorsal process, which are aligned together to a tapering prong wedged between the septomaxillaries (Figs. 2.5A, 2.12, 2.22). A much broader ventral process extends for the same distance in posterior direction on the flank of the crest and is surrounded by the septomaxilla, nasal, and maxilla (Figs. 2.5C, 2.10). The suture with the maxilla runs anteroventrally towards the posterior snout constriction, and in all specimens a conspicuous posteriorly pointing prong is present close to the alveolar border. In ventral view, the premaxillaries are in contact over much of their length. Just after the downturned tip, they form an oval depression that leads into the narrow foramen incisivum (Figs. 2.5B, 2.13, 2.23). Beginning at the level of the fourth premaxilla tooth, the prominent, half-cylindrical alveolar ridge runs medially along the tooth row towards the maxilla. The alveolar ridges of both premaxillaries enclose an interpremaxillary fossa. Posteriorly, the premaxilla tapers into a short, lamellar palatal process that the overlaps the maxilla laterally and underlies the vomer posteriorly. Both processes approach the choana but neither touch the palatine nor contribute to the border of the internal naris (Fig. 2.9).

Maxilla. The maxilla forms the laterally expanded, posteroventral part of the snout. In dorsal view, the bone is composed of the anteriorly tapering body and two posteriorly directed processes which surround the anterior two third of the antorbital fenestra. The dorsal process is thin and runs in posterodorsal direction to meet the lacrimal (Figs.

2.5C, 2.15). The dorsal rim contacts the nasal along the base of the nasal bulb in a serrated suture (Figs. 2.5C, 2.10). The broad and massive ventral process has a convex outline which results in the flared posterior part of the snout. It contacts the jugal posteroventrally and, with exception of SMNS 5725 (Fig. 2.2.43B), the lacrimal posterodorsally.

In ventral aspect (Figs. 2.9, 2.13, 2.16, 2.23), the alveolar ridge of the premaxilla continues on the maxilla along the bulging tooth row and finally merges with the flat ventral surface at the level of the anterior part of the choanae. The suture with the premaxilla runs in the narrow groove between the anterior maxilla teeth and the palatal ridge, and crosses the latter obliquely with the expansion of the maxilla. The palatal wing of the maxilla is overlapped by the premaxilla and the tip of the palatine and slopes downwards in posteromedial direction towards the choana. Because of poor preservation in that area, the contact to the vomer is usually obscured, but it seems likely from SMNS 5725 (Fig. 2.13) that the palatal wing of the maxilla borders the choana anteriorly and makes contact with the vomer medially. This would be in accord with the pre-choanal area reconstructed for the majority of phytosaurs (e.g. CAMP 1930; CASE 1929). In BMNH 42743, however, there is little evidence for such a configuration (Fig. 2.23), and the most likely reconstruction shows the maxilla excluded from the choana by a contact of premaxilla and palatine. The matter has to await better preserved material, although the other specimens support the conservative reconstruction. Laterally, the maxilla is united with the palate by an interdigitating suture and enters the anterior border of the suborbital fenestra. Posteriorly, it meets the ectopterygoid and the jugal.

Septomaxilla. Among other characters, phytosaurs are characterised by a pair of well developed and externally visible ossifications of the narial region, by convention identified as septomaxillae. It is evident, however, that the bone internally is much more complex, and shows highly differentiated connections with the premaxilla and the nasal (CAMP 1930). Although I am aware that SERENO (1991) listed a number of structural and positional differences of the phytosaur septomaxilla to the septomaxilla of squamates and early synapsids, and probably correctly questioned the homology of these ossifications, the name is retained here for the lack of a plausible alternative. Without invasive examination, *Nicrosaurus kapffi* can contribute little to this discussion. The elements in question are developed as conspicuous, elongated bones on the dorsal surface of the snout anterior to the nares (Figs. 2.5A, 2.8, 2.12, 2.15, 2.22). In all specimens, they extend far beyond the anterior tip of the nasals. The septomaxillae are in contact over most of their length. An anterior extension of the septomaxilla separates the dorsal from the ventral process of the premaxilla. The lateral side of its posterior half also contacts the nasal. The septomaxilla borders the anterior tip of the naris and meets the nasal in the

anterior third of the internarial septum. From this point, the suture descends posteroventrally at a low angle (SMNS 5725: Fig. 2.14). Thus, the septomaxillae form most of the internarial septum.

Nasal. The nasals are long and broad bones that form the posterodorsal part of the prenarial crest including the laterally bulging nasal bulb. Below and anterior to the naris, the exposure of the nasal is limited to the flanks of the crest. It sends forward a short, but broad process which bifurcates the ventral process of the premaxilla. Anteroventrally, the nasal meets the dorsal process of the maxilla in a complex serrated suture. Thus the bone usually does not contribute to the antorbital fenestra (however, see variation, 2.2.5). The nasal-maxilla suture runs in the infranasal recess that separates the nasal bulb from the expanded posterior part of the snout (Figs. 2.5C, 2.10, 2.24), but is often fully or partially obliterated by the sculpture of that recess (Fig. 2.14). Most of the dorsal surface of the interorbitonasal area is covered by the nasal, and it is at least superficially exposed on the posterior two thirds of the internarial septum in one specimen, SMNS 5725 (Fig. 2.14). Posteroventrally, the bone meets the lacrimal and the prefrontal and is connected to the frontal in a deeply interdigitating suture.

Frontal. The frontals are the largest bones of the skull roof situated between both orbits. Anteriorly, they join the nasals in a transverse, deeply serrated suture. The joints to the prefrontals anterolaterally and the postfrontals posterolaterally show a more undulating course (e.g. Fig. 2.12). A broad lateral process extends between the pre- and postfrontal to form the dorsal border of the orbit, which results in the cross-shaped outline of the both articulated frontals. Posteriorly, the frontals meet the parietals.

Parietal. The parietal meets the frontal anteriorly and the postfrontal anterolaterally. The bone shows a broad contact with the postorbital laterally and thus forms the anterior border of the supratemporal fenestra. The lateral part of the parietal slopes down vertically to meet the laterosphenoid and the epiotic (Fig. 2.7). Thus, it forms the medial wall of the supratemporal fenestra and merges posteriorly with the squamosal process.

The squamosal process of the parietal is directed posterolaterally and in dorsal view, both processes together form a complex of two lamellae set in an angle that opens posteriorly (Fig. 2.41). The apex of the angle is rounded and bears a shallow parietal fossa that runs ventrally onto the supraoccipital shelf (also Figs. 2.8, 2.11, 2.18). The medial part of the process is developed as a straight and thin, sharp-edged plate that rides on the supraoccipital. Here, both surfaces of the process slope steeply in anterolateral direction. This results in a slight overhang of the squamosal process over the supraoccipital shelf. In occipital view, a thin, crescent-shaped lamellar extension of the

squamosal process reaches downward onto the supraoccipital shelf overlying the supraoccipital (SMNS 5726: Fig. 2.11; SMNS 54706: Fig. 2.21B). The shape and position of this lamella is similar to a discrete element identified as tabular by CAMP (1930) in *Smilosuchus gregorii*. In *Nicrosaurus kapffi*, however, there is no unambiguous evidence of a sutural separation of the lamella onto the shelf and the vertical squamosal process, and therefore both structures are regarded here as part of the parietal (see discussion in part 3.3.3.3). The dorsal edge of the inclined medial part of the squamosal process curves strongly downwards and in its lateral part, the process becomes a flat, horizontal tongue. It overlies the parietal process of the squamosal and terminates at about the mid-point on the parieto-squamosal bar. According to SMNS 5726 (left side), the squamosal process of the parietal does not reach the posttemporal fenestra as in *Nicrosaurus* species B BMNH 42745.

Circumorbital elements:

Lacrimal. The lacrimal is an elongated, anterolaterally oriented bone between the orbit and the antorbital fenestra. A consistent feature of *Nicrosaurus kapffi* (and *Nicrosaurus* species B) is the presence of an elongated depressed area on the surface of the lacrimal that links both openings. Here, the bone is sculptured with prominent, short ridges and the dorsal limitation of the area frequently obscure the joints of the adjacent prefrontal with the jugal (e.g. SMNS 5725: Figs. 2.12, 2.14). Because of either deformation or the presence of matrix, the opening of the lacrimal canal, which is usually placed internally in the anteroventral corner of the orbit (CAMP 1930; CASE 1929) at the joint of lacrimal and prefrontal (CASE & WHITE 1934; WITMER 1997), can not be confirmed. Anteriorly, the lacrimal is usually bifurcated (Figs. 2.5A, 2.8). A process situated ventrally to the antorbital fenestra joins the maxilla anteriorly and the jugal ventrally. A more slender dorsal process runs forward between the nasal and the posterior third of the antorbital opening to join the dorsal process of the maxilla. The lacrimal meets the prefrontal posterodorsally and touches the postorbital posteriorly below the orbit.

Prefrontal. This is a small subrectangular bone in the anterodorsal corner of the orbit. The prefrontal is surrounded by the nasal anteriorly, the jugal ventrally, and the frontal medially and laterally.

Postfrontal. The postfrontal is usually the smallest dermal skull element, which forms the posterodorsal border of the orbit. It joins the frontal anteromedially and is bound by the postorbital posteroventrally and the parietal posteriorly.

Postorbital. On the skull roof, the postorbital joins the postfrontal anteromedially and is united with the parietal in a longitudinally directed suture. Therefore, the bone not only forms the anterior half of the lateral border of the supratemporal fenestra, but also contributes a little bit to its anterior rim.

The postorbital sends a ventral process, which is the dominant bone of the postorbital bar, forward and downward to about half the height of the infratemporal fenestra. The ventral process is remarkably slender in lateral view, but approximately twice as deep. In posterior view, the process bifurcates to receive the dorsal process of the jugal (SMNS 54706: Fig. 2.21B). Anteroventrally, the process usually makes contact with the lacrimal preventing the jugal from contributing to the orbit (but see variation, 2.2.5). Thus, the postorbital borders much of the orbit posteriorly and posteroventrally, as well as the infratemporal fenestra anterodorsally.

Posteriorly, the squamosal process of the postorbital forms the anterior part of the postorbito-squamosal bar and meets the squamosal in a tongue-like, interdigitating suture (Figs. 2.5A, 2.8, 2.15).

Temporal elements:

Jugal. The jugal is a triradiate and, compared to the other skull elements, thin bone. Anteriorly, it contacts the maxilla by means of a thin bony lamella that underlies the bone. In external view, the suture is convex with the apex pointing anteriorly (SMNS 54706: Fig. 2.21A). The postorbital process of the jugal runs posterodorsally along the maxilla to meet the postorbital and lacrimal. In some specimens, the jugal separates the lacrimal from the postorbital and contributes to the orbital rim (see variation, subsection 2.2.7). There is a deep, rounded ridge running along the internal posterior margin of the postorbital process of the jugal (internal ridge or medial spine *sensu* CAMP 1930), which is aligned with the ventral process of the postorbital (Fig. 2.21B). Thus, a long recess is developed in the anteroventral part of the postorbital bar. The dorsal process of the ectopterygoid extends medially along this ridge. From the posterior surface of the ridge, a thin and sharp lamella projects backwards into the infratemporal fossa (Fig. 2.21A). The lamella is not as prominent as in *Mystriosuchus* (HUENE 1911: pl. 13 fig. 2) and does not continue onto the postorbital as in *Smilosuchus* (ANDERSON 1936). According to ANDERSON (1936), the lamella served to span a fascia for the M. adductor mandibulae externus. In a deep recess in the internal corner of the infratemporal fenestra formed by jugal and ectopterygoid, a foramen opens into the jugal. A much smaller, crescent-shaped recess is located in the same position on the external surface of the jugal (Fig. 2.21A). It is probably homologous with the extensive pre-infratemporal shelf seen in *Mystriosuchus*. The posterior process of the jugal forms much of the ventral border of

the infratemporal fenestra. The contact with the quadratojugal is a highly complex suture: the plate-like process of the jugal is wedged between two lamellae of the dorsally placed quadratojugal and largely hidden from lateral view (SMNS 54706, BMNH 42743), as in *Smilosuchus gregorii* (CAMP 1930). However, in ventral view the jugal extends far backwards reaching almost the lateral condyle of the quadrate (Figs. 2.5B, 2.16, 2.21B, 2.23).

Quadratojugal. The quadratojugal is a subtriangular bone in the posteroventral edge of the skull that covers much of the lateral aspect of the quadrate and jugal (Figs. 2.10, 2.22, 2.23). The dorsal tip terminates at about half the height of the infratemporal fenestra, where it contacts the squamosal dorsally and anterodorsally. Posterodorsally, the dorsal extension of the quadratojugal is recessed leaving the quadrate exposed on the lateral side of the skull. The anterior process of the quadratojugal runs forward along the posterior third of the infratemporal fenestra and is firmly connected to the jugal as described above. Externally and internally, the sutures are deeply interdigitated, and are running in posteroventral direction in a low angle. Thus, the quadratojugal is actually excluded from the ventral edge of the skull, except for a short distance in front of the quadrate. In posterior aspect, the dorsal part of the quadratojugal is developed as a sharp ridge, the medial slope of which leads into the deep recess of the quadrate foramen (Figs. 2.17, 2.21B, 2.41).

Quadrate. The quadrate is a large bone, that forms the load-bearing element of the cheek and the temporal region. In posterior view, the quadrate is the most prominent skull element (Fig. 2.41). The lateral face of the quadrate, however, is largely hidden by the quadratojugal and the squamosal. Only the posterolateral part of the quadrate head, which leads into the tympanic fossa, and the lateral condyle are exposed in lateral view (Fig. 2.40).

The quadrate head rests firmly in a star-shaped recess formed by the ventral and medial plane of the body of the squamosal (BMNH 38043). Posteriorly from the joint, it is deeply excavated to form the tympanic fossa along the anteromedially running, interlocking suture with the paroccipital process of the opisthotic. Laterally, the quadrate head is braced firmly against the base of the paroccipital process of the squamosal (Figs. 2.11, 2.17).

The pterygoid wing of the quadrate is illustrated in the Figures 2.11, 2.17, and 2.25. The base of the broad pterygoid wing is strongly built, but soon the wing tapers to a thin and high lamella. Its medial side articulates with the quadrate wing of the pterygoid to form the major part of the large pterygo-quadrate plate. The plate runs forward in anteromedial direction and is inclined laterally to such a degree, that its posterior surface

faces posteromedially and upward. The ventral part of the pterygo-quadrate plate is deflected medially to form a thin, almost horizontal shelf. The shelf connects the basisphenoid process of the pterygoid with the body of the quadrate and reaches a maximum width of 25 mm next to the quadrate body. Thus, a deep vertical recess is formed where the pterygoid wing of the quadrate merges with the condylar part of the bone. The recess shallows in dorsal direction and the dorsal part of the pterygoid wing is more confluent with the quadrate head meeting it in a rounded angle. The presence of a shelf accounts for the broad pterygo-quadrate bar in ventral aspect. On the pterygoid wing of the quadrate, the edges of the pterygo-quadrate bar are somewhat raised and may enclose a fossa (Fig. 2.41).

The posterior aspect of the quadrate (Fig. 2.41) is of triangular outline and the body of the bone is offset from the pterygoid wing by a vertical, rounded edge. The condylar portion of the quadrate articulates with the quadratojugal laterally. Towards the quadrate head, the quadrate narrows consistently and shows a lateral emargination to accommodate the quadrate foramen at the suture with the quadratojugal. This is probably a zone of restricted rigidity, since at this point all complete skulls of *Nicrosaurus kapffi* suffered from *post-mortem* fracturing caused by the compaction of the sediment (e.g. Fig. 2.17).

The articular surface of the quadrate is greatly elongated in transversal direction and the former extent of its cartilaginous cap is marked by a conspicuous rim. Both the lateral and medial condyles are not well demarcated, but rather somewhat enlarged terminal areas of the facet, which results in a short and wide, saddle-shaped lower jaw joint. The medial condyle is clearly set off from the pterygoid wing of the quadrate (Fig. 2.11), whereas the lateral condyle is more confluent with the ventral edge of the cheek.

Squamosal. In phytosaurs, the squamosal is a highly complex bone. It is the most conspicuous bone of the temporal region in advanced forms, and because of its supposed significance for taxonomy and phylogeny it has received much attention. The squamosal consists of the squamosal body and at least five processes, depending on the opinion of each worker about the individuality of the processes. In previous descriptions, the various processes have been named inconsistently and sometimes almost similar terms have been used for different structures of the squamosal. To avoid further confusion, the six processes of the squamosal identified in *Nicrosaurus kapffi* are introduced here according to the elements to which they establish contact:

(i) the postorbital process (synonym: upper anterior process, CASE 1929),
(ii) the parietal process (synonyms: lower anterior process, CASE 1929; 4th process, CAMP 1930),
(iii) the pterygoid process (synonym: 5th process, CAMP 1930),

(iv) the quadratojugal process (synonyms: descending process, CASE 1922, 1929; anteroventral process, CAMP 1930),
(v) the paroccipital process (synonyms: posterior descending process, CASE 1929; descending process, LONG & MURRY 1995; inferior process, MEHL 1916; hook-like process MEHL 1913, 1928b, and most recent authors), and
(vi) the posterior process.

One of the autapomorphies of phytosaurs is the marked separation of the squamosal in a horizontal dorsal and vertical lateral plane (LONG & MURRY 1995). The squamosal body is defined here as the central part of the bone that articulates medially and ventrally with the quadrate. The body is morphologically confluent with the postorbital process and the posterior process, and a discrimination between these three parts is admittedly somewhat arbitrary. Medial to the quadrate head, the horizontal plane of the squamosal is drawn out to overhang the supratemporal opening (Fig. 2.11). In marked contrast to *Leptosuchus* and *Smilosuchus*, the vertical part of the squamosal body as well as the posterior process is low.

The postorbital process is the short anterior extension of the squamosal body that meets the postorbital in a deeply concave suture. Its lateral rim, the posterodorsal border of the infratemporal fenestra, is thickened and gently rounded, whereas the part of the process medial to the lateral rim is flattened dorsoventrally. This is the part of the skull roof that (in combination with the medial part of the squamosal body) accounts for the width of the postorbito-squamosal bar and overhangs and narrows the supratemporal opening considerably (Figs. 2.11, 2.41).

The parietal process is a broad and thin tongue of bone directed anteromedially. It meets and underlies the squamosal process of the parietal to form the parieto-squamosal bar (Figs. 2.6, 2.11). I was unable to determine the exact lateral extent of the parietal process in the specimens. In SMNS 4378, there is an medioventral extention of the base of the parietal process that lies on the posterior face of the paroccipital process of the opisthotic and contributes considerably to the ventral border of the posttemporal fenestra (Fig. 2.6). In anterior view, this extension can be seen covering a part of the internal aspect of the paroccipital process of the opisthotic as well, indicating that the extension embraces the paroccipital process from above (Fig. 2.7). Unfortunately, the reconstruction cannot be corroborated in the other specimens of *Nicrosaurus kapffi*, in which either the paroccipital process is not freed of matrix posterolaterally (SMNS 4379, SMNS 5726), or the sutural connections of the bones around the posttemporal fenestra are not preserved (SMNS 5725, SMNS 5727, SMNS 54708, BMNH 43743). The intimate contact of squamosal and paroccipital process has already been described by MEYER (1863: pl. 42 fig. 4), but the evidence from SMNS 4378 was neglected in

subsequent reconstructions (MCGREGOR 1906: fig. 4 based on SMNS 5727, and copies reproduced in subsequent studies), perhaps to achieve more similarity with the "normal" condition among phytosaurs like *Mystriosuchus planirostris*, the main subject of MCGREGOR's study. The parietal process continues in form of a ridge posteriorly onto the ventral surface of the posterior process, terminating at the extremity of the squamosal (Figs. 2.11, 2.16, 2.19, 2.21B).

A thin splint of bone at the dorsal rim of the pterygo-quadrate plate of SMNS 4378 could represent the pterygoid process of the squamosal, according to a process of the squamosal in a similar position in *Smilosuchus gregorii* (CAMP 1930). It extends along the ventral border of the pteroccipital fenestra for about half the length of the opening (Fig. 2.7). The point of insertion at the squamosal body can not be determined in the material available. A similar process is not visible in the other specimens; however, in *Smilosuchus* the pterygoid process is hidden between laminae formed by the pterygoid and the quadrate (CAMP 1930: fig. 30), and this might explain its superficial absence.

The quadratojugal process proceeds downward and forward and finally terminates braced against the internal surface of the quadratojugal. The process shows a broad contact with the body of the squamosal, but the dorsal part of the posterior rim is deeply concave and the underlying quadrate is exposed. In lateral view, the tapering anteroventral part of the process is visible along the dorsal third to, at most, half of the infratemporal fenestra.

The paroccipital process is a downward pointing, massive and knobbly structure. The base of the process is firmly sutured with the paroccipital process of the opisthotic (Fig. 2.17). In lateral view, the paroccipital process of the squamosal is generally lancet-shaped and compressed laterally, but the exact morphology varies in individuals in the presence of irregular grooves and smaller protuberances (Figs. 2.10, 2.11, 2.17, 2.20). The paroccipital process is probably the site of origin for the M. depressor mandibulae profundus (ANDERSON 1936), and a varying degree of ossification of its tendon could account for the different shapes.

The posterior process is the broad extension of the squamosal body that overhangs the edge of the skull (i. e. the lateral extremity of the postorbito-squamosal bar) for about 30 mm. In dorsal view, this part of the squamosal is somewhat produced laterally and ventrally, and includes a laterally facing, crescentic muscle scar for the M. depressor mandibulae superficialis (ANDERSON 1936), placed dorsally of the paroccipital process of the squamosal (Fig. 2.20). The medial rims of the posterior processes are parallel or slightly diverging in all specimens except one (SMNS 5727: Fig. 2.18) and terminate perfectly rounded in the shape of a logarithmic curve (in contrast to the statement in LONG & MURRY 1995: 61). The posteroventral view of the posterior process is illustrated in Figure 2.11. In this view, the tip of the squamosal is crowned by a broad, ventrally

protruding knob. The medial rim of the posterior process is thickened, and in its posterior part the rim is even flattened and rugose towards the tip in SMNS 4379 and SMNS 5727 to form a posteromedially and ventrally facing area. Medial to the thickening, a large upper sulcus is developed on the ventral surface of the posterior process which opens anteriorly to the horizontal part of the body and postorbital process overhanging the supratemporal fenestra. A narrow and much deeper ventral sulcus is situated on a lower level between the opisthotic and the parieto-squamosal bar. Finally, there is a small triangular recess aligned with the parieto-squamosal bar separated from the upper sulcus by the posterior ridge-like extension of the parietal process. Laterally, the recess is bordered by the vertical connection of the paroccipital process and the terminal knob.

Palate:

Vomer. Only little is exposed of the vomers on the palate, forming the interchoanal septum and a small area in front of the choanae. The rhomb-shaped anterior third of the vomers appears to be fused in all specimens. This part separates the posterior palatal extensions of the premaxillaries and its shape leads to the divergence of the anterior tips of the choanae. Laterally, the vomers probably make contact with the maxillaries (indicated in SMNS 5725: Fig. 2.13), and thus do not contribute to the anterior rim of the choanae. The ascending parts of the vomers that form the external walls of the interchoanal septum are not exposed in the specimens. However, preparational damage of the interchoanal septum in SMNS 5726 confirms that both vomers are actually very thin and U-shaped in cross-section, and cover another bone, probably two similar aligned lamellae belonging to the pterygoids (comp. CAMP 1930: fig. 32 and CASE 1929: fig. 17c). The vomers continue for some distance behind the choanae, thus bordering the choanae posteriorly. They meet the palatines laterally and posterolaterally, and their posterior extremities make contact with the pterygoids at a point in mid-line of the palatal vault (SMNS 4379: Fig. 2.9).

Palatine: In ventral view, the palatine is subdivided into a ventral plate, the medial section of the palatal plane, and into a medial wing that occupies the anterolateral and lateral area of the palatal vault. The description is largely based on SMNS 4379, illustrated in Figure 2.9.

The tapering tip of the ventral plate overlies the maxilla and terminates well beyond the choana. In posterior direction, the palatine expands laterally along the serrated suture with the maxilla. It forms the medial border of the suborbital fenestra and makes contact with the ectopterygoid posterolaterally. The ventral plate of the palatine is convex along a sagittal axis and forms a distinct rim to the palatal vault, which was named the "palatine

ridge" (MCGREGOR 1906) or "palatal ridge" (CASE 1922). The anterior part of the medial rim is strongly bent upward to a medially bulging wall bordering the choana. Starting at a medially pointing prong, the rim is developed as a thin sharp lamella overhanging the posterior two thirds of the choana, and the palatal vault. Posterior to the choana, the overhang turns into a posterolateral direction and becomes more prominent. It then changes gradually to a rounded ridge, which merges with the downturned ventral wing of the ectopterygoid, and from which the medial wing raises onto the palatal vault (see also Figs. 2.14, 2.16 and 2.23). Additionally, the surface of the ventral plate shows three different structures. A broad longitudinal bulge, corresponding to CAMP's (1930) "palatal axis", is running in the posterior part along the medial rim. Several shallow ridges are crossing the width of the plate in the anterior and central part. On the overhang of the medial rim, there is an array of weak longitudinal ridges associated with pits in two specimens (SMNS 4379: Fig. 2.6; SMNS 5725), which open in posterior direction. These structures might represent muscle scars and tendon insertions.

Since MCGREGOR (1906), the medial overhang of the palatines and the palatine ridge have been interpreted as indicators of a soft tissue structure spanning over the choanae and the palatal vault. It is indeed likely that such a secondary palate was developed, of which the overhang is interpreted as an incipient peripheral ossification.

The medial wing of the palatine ascends upward from the posterior part of the palatine ridge and forms the lateral wall of the palatal vault. In the anterior half of the palatine in BMNH 42743 (right side), the medial wing ascends vertically and thus forms the lateral wall of the air passage between naris and choana. It probably continues under the overhang of the palatine plate, but this area is usually not freed from matrix. The medial and caudal part of the medial wing is overlain by the pterygoid, but in ventral view the palatines are still visible and contribute to the roof of the palatal vault (also visible in Figs. 2.16 and 2.23). This is evident in the anterior part close to the suture with the vomer, where the wing is produced to a medially tapering process that meets its counterpart at the mid-line of the palate.

Pterygoid. The large dorsal wings of the pterygoids cover much of the central and posterior roof of the palatal vault, slightly overlapping the medial wings of the palatines laterally and anteriorly (Fig. 2.9). Here, both pterygoids meet in an interpterygoidal fissure along the mid-line of the skull, in all specimens a deep cleft infilled with sediment (Figs. 2.9, 2.13, 2.19, 2.23). A cross-section in SMNS 5725 shows that the pterygoids meet at the bottom of the fissure. The interpterygoid fissure is probably the vestige of the anterior part of the interpterygoid vacuity that has been closed secondarily. The bones then diverge towards the base of the ectopterygoid process, leaving open a minute interpterygoid vacuity. The posterior rim of the dorsal wing is turned ventrally to form a

prominent sharp ridge connecting the dorsal wing with the posterior rim of the ectopterygoid wing (Fig. 2.25).

Posterolaterally, the pterygoid descends steeply to the ectopterygoid wing, which forms together with the ectopterygoid the rounded, posteroventrally projecting pterygoid flange. The base of the flange is broad and unconstricted (Fig. 2.25). In ventral view, much of the ectopterygoid wing is covered by the ectopterygoid, and for this reason the pterygoid is only visible at the medial base and the distal extremity of the joint structure (Figs. 2.16, 2.23).

The base of the basisphenoid process joins broadly the dorsal wing and the base of the quadrate wing of the pterygoid (BMNH 42743: Fig. 2.25). The distal extremity of the process is separated from the base by a stout neck-like constriction. It is expanded to form a thin slightly concave articular surface with a number of peripheral projections, that receives the basipterygoid process of the basisphenoid. The joint area faces dorsolaterally.

The quadrate wing of the pterygoid is described according to SMNS 5726 (Fig. 2.17) and BMNH 42743 (Fig. 2.25). The wing is divided into a dorsal and a ventral process, which are distinguishable from the adjacent quadrate by their raised relief. The dorsal process runs posterodorsally and borders the pteroccipital fenestra. Since in SMNS 5726 the tip of the process is broken off at a point 10 mm in front of the quadrato-opisthotic suture in the tympanic fossa, the exact length is indeterminable. The ventral process covers most of the occipital surface of the shelf formed by the pterygo-quadrate plate and extends into the recess on the quadrate. It is possible that both processes once had been connected by a sheet of bone which broke off *post-mortem*. This could explain the relief of the suture present in both specimens as well as the granular surface of the underlying quadrate between both processes in BMNH 42743. In the reconstruction (Fig. 2.41), the quadrate wing of the pterygoid is exactly illustrated as preserved in SMNS 5726. In ventral view, there is a bean-shaped recess situated in the corner formed by the quadrate wing and the ectopterygoid wing of the pterygoid, which expands posteriorly to a broad and shallow fossa on the ventral face of the quadrate wing (Fig. 2.9), very similar to the fossa on the pterygoid wing of the quadrate. The zigzag-shaped suture between pterygoid and quadrate crosses the pterygo-quadrate bar obliquely and is somewhat raised, separating both fossae on pterygoid and quadrate (Figs. 2.11, 2.17). At the base of the quadrate wing, a sulcus is floored by the pterygo-quadrate bar and the ascending pterygo-quadrate plate dorsolaterally (freed in BMNH 42743 only: Fig. 2.25).

Probably inspired by his findings in *Mystriosuchus* species B, HUENE (1911: figs. 14-16) presented a reconstruction of the left quadrate wing in SMNS 5726, in which the pterygoid extends far posteriorly over the quadrate and borders the foramen quadrati. This is a highly unusual construction for an archosaur, and already MEHL (1916) and

CASE (1920, 1929) expressed their doubts about the validity of HUENE's claim without having examined the specimen. The "suture" between pterygoid and quadrate as indicated by HUENE (1911: figs. 14) actually corresponds to a prominent fracture horizontally across the quadrate (see Fig. 2.7), which is evidently not present in SMNS 54706 (Fig. 2.21B), and even on the right quadrate of SMNS 5726 as well. Likewise, the suture shown in his figure 15 is composed of a series of microfractures (indicated in Fig. 2.17) arbitrarily selected on the pterygo-quadrate plate. It is obvious that Huene misinterpreted fractures, which can be found frequently in almost similar positions across the quadrate and pterygo-quadrate plate in a number of phytosaur skulls, including *Nicrosaurus kapffi* but also both species of *Mystriosuchus* (pers. obs.). The shape and size of the quadrate wing of the pterygoid in *Nicrosaurus kapffi* is actually very similar to other well known phytosaurs (e.g. CAMP 1930: pl. 2a, pl. 6; this study, Fig. 3.5).

Ectopterygoid. The ventral wing of the ectopterygoid covers most of the downward projecting wing of the pterygoid. Following the twisted shape of this projection, the ventral wing is convex in an anteromedial direction. The medial suture of the wing with the pterygoid and the palatine runs in a longitudinal groove towards the suborbital fenestra (Fig. 2.9). Towards the base of the wing, the thickness of the ectopterygoid increases, and narrows to a neck-like transition to the palatal part of the bone. This part of the ectopterygoid spreads out anterolaterally to a triangular and horizontal surface. It borders the lateral side of the suborbital fenestra and meets the maxilla anterolaterally. Laterally, the bone contacts the lacrimal, and contributes to the anterior border of the infratemporal fenestra. The ectopterygoid sends a triangular jugal process upward along the medial side of the jugal, that almost reaches the ventral tip of the postorbital (SMNS 54706: Fig. 2.21B). There is no indication in the material under study that the ectopterygoid, palatine, and pterygoid were pneumatised by an "ectopterygoid canal" nor are there any recesses present as in a number of other phytosaur species (*Angistorhinus talainti*: DUTUIT 1977a; *Brachysuchus megalodon*: CASE 1929; *Rutiodon carolinensis*: DOYLE & SUES 1995; *Smilosuchus gregorii*: CAMP 1930).

Occipital elements and braincase:

Supraoccipital: The supraoccipital forms a concave, hemicircular supraoccipital shelf below the parietals (Fig. 2.41). The dorsolateral area of the shelf is covered to a various degree by the descending laminae of the squamosal processes of the parietals. This results in both that the external outline of the supratemporal on the supraoccipital shelf is triangular and that the apex of the triangle does not reach to the level of the skull

roof. In the extreme, the parietals can form the entire upper half of the supraoccipital shelf (SMNS 4379). In two specimens (SMNS 5727, SMNS 54706), there is a distinct knob or rugosities, probably the insertion of a tendon, located under the parietal overhang (Figs. 2.21B, 2.41), from which, as in the other specimens, a faint median ridge runs down the supraoccipital shelf (Fig. 2.21B). The lateral parts of the supraoccipital touch at least the medial corner of the posttemporal fenestra (SMNS 4378; SMNS 5726). SMNS 5726 suggests furthermore, that the bone extends into a low but broad flange that underlies the medial half of the parieto-squamosal bar, and perhaps borders a considerable distance of the posttemporal fenestra. This interpretation depends on the unknown length of the parietal process of the squamosal. The suture with the exoccipitals is located on a concave sharp ridge that spans between both parieto-squamosal bars and marks the ventral border of the supraoccipital shelf. As reconstructed in Figure 2.41, the suture crosses the edge and participates in roofing the foramen magnum, however, the configuration of this region is subject to individual variation (subsection 2.2.5.2).

CAMP (1930) identified an unpaired postparietal covering as a superficial bony plate most of the supraoccipital shelf in *Smilosuchus*. In SMNS 4379, there is evidence for a faint ridge-like step in the same position as CAMP's postparietal-supraoccipital suture, suggesting at first glance that a thin lamina overlies the dorsal part of the supraoccipital. However, this step is not continuous but broken up into an array of shorter ridges and is lacking altogether in some specimens. It is concluded, that there is not sufficient evidence to postulate a separate ossification and that the centre of the supraoccipital shelf is formed by the supraoccipital alone (see also discussion in *Mystriosuchus* species B, part 3.3.3.3).

Exoccipital: The exoccipitals (Fig. 2.41) surround almost the entire foramen magnum. The bones meet ventrally along the midline, but diverge toward the basioccipital condyle to allow the basioccipital to participate in forming the floor of the foramen magnum. The rounded sutures of the exoccipitals with the basioccipital are clearly discernible in the dorsolateral areas of the occipital condyle only (e.g. Fig. 2.25). No specimen currently available shows sutures separating the exoccipital from the ventrally placed elements, the anterior part of the basioccipital, and the basisphenoid, which suggests that all three bones are fused in the region of the neck of the condyle. Laterally, there is no distinction between the occipital face of the exoccipital and the opisthotic (e.g. Fig. 2.6), and it seems that both bones are completely fused externally to form most of the base of the paroccipital process. There are two roughened, poorly outlined areas placed symmetrically above and lateral of the foramen magnum, which could represent the joints of the proatlas as in *Nicrosaurus* species B SMNS 12593. The

contribution of the exoccipital to the paroccipital process is described in more detail below.

Basioccipital: The posteriormost limit of the basioccipital condyle lies slightly in front of a transverse line drawn through the glenoid surfaces of the quadrates. The hemispherical condyle points posteriorly, but the centre of the articular surface to the atlas faces posteroventrally. The neck of the basioccipital condyle is short and stout. Several nutrient foramina are placed in the neck area of the basioccipital (Fig. 2.25). A singular foramen lies in the corner formed by the tubera and the neck of the basioccipital (BMNH 42743: Fig. 2.25), in SMNS 4379 at the end of a short and shallow groove formed by two anteroventrally converging ridges on the ventrolateral face of the neck of the occipital condyle. In the same specimen, a number of foramina are placed on the ventral face of the basioccipital neck. In front of the neck, the bone expands abruptly in lateral and ventral direction, reaching about twice the width of the condyle, to form the prominent and well separated basal tubera (Figs. 2.11, 2.16, 2.19, 2.25). The suture with the basisphenoid is located in a transverse, broadly undulating groove on the rugose surface, separating the tubera in two almost similar sized basioccipital and basisphenoidal portions. Each tuber is roughly oval shaped, and both are separated by a deep median cleft. The ventral surface showing the irregular, deep rugosities for the Mm. basioccipitovertebralis and occipitotransversalis profundus faces ventrally and somewhat posteriorly.

Epiotic. A small ossification is exposed in SMNS 4378 on the surface of the braincase medial to the posttemporal fenestra and posterodorsally to the otic bones (Fig. 2.7). Based on positional and structural criteria, the bone is identified as the epiotic (see *Mystriosuchus* species B, part 3.3.3.3). CAMP (1930) and CHATTERJEE (1978) attributed the same ossification centre to the supraoccipital because of an indistinguishable fusion between both elements in their specimens. Since such a fusion cannot be demonstrated in *Nicrosaurus kapffi*, the epiotic is treated here as separate entity. The epiotic is well distinguished by sutures from the surrounding bones, in contrast to the complete fusion of the respective ossification in the braincase of "*Parasuchus*" (CHATTERJEE 1978) and *Brachysuchus* (CASE 1929). The bone is surrounded by complex sutures with the opisthotic ventrally and the parietal dorsally, and touches the prootic anteriorly. It makes also contact to the parietal process of the squamosal.

Opisthotic and paroccipital process: The neurocranial part of the opisthotic is confined to the posteroventral wall of the braincase. Dorsally, it is united with the epiotic in a horizontal, indentated suture that runs into the medial corner of the posttemporal

fenestra. A posteriorly sloping contact to the prootic limits its exposure anteriorly and ventrally (Fig. 2.7).

The opisthotic is strongly expanded laterally to form the paroccipital process together with the prootic, exoccipital, and squamosal. In ventral view, the base of the paroccipital process bears two well distinguished crests (Figs. 2.11, 2.17, 2.25). The shorter and medially placed crista was termed the opisthotic lamella (synonym of the crista interfenestralis in more derived archosaurs) by WALKER (1990) or crista paroccipitalis (CHATTERJEE 1978). The opisthotic lamella runs along the mid-line of the paroccipital process and separates the foramen jugulare or metotic fissure (the exit of the nervi IX-XI, and the vena jugularis) and the adjacent jugular groove from the somewhat broader stapedial groove leading to the foramen ovale. The opisthotic lamella and the lateral ridge of the stapedial groove are sharp-edged and low in comparison to *Nicrosaurus* species B, but more prominent than in *Mystriosuchus*. A distinct exit of the nervus hypoglossus (XII) on the exoccipital pillar is not present, which might indicate that the foramen nervi hypoglossi is integrated in the recess that houses the foramen jugulare (compare *Nicrosaurus* species B). However, all specimens need further preparation in that area and details of both the foramina jugulare and ovale are not available. The posterolateral suture of the opisthotic with the prootic is visible for a short distance on the medial flank of the crest that demarcates the stapedial groove laterally, until it disappears on the paroccipital process (Figs. 2.17, 2.25). Thus, the foramen ovale at the ventral base of the paroccipital process is still bound by the prootic anteriorly, and the bone forms most of the lateral ridge that demarcates the stapedial groove. Preservation is too poor to allow confirmation, but the course of the suture seems to indicate that the foramen jugale is completely enclosed in the exoccipital/opisthotic complex, but the prootic participates in surrounding the foramen ovale.

The paroccipital process reaches from the foramen magnum in posterolateral direction towards the squamosal (Figs. 2.5B, 2.11, 2.16, 2.19, 2.21B, 2.23). The base of the paroccipital process is wide anteroposteriorly to accommodate the jugular and stapedial grooves (Figs. 2.11, 2.25), however, the expansion is not that great as it appears in *Nicrosaurus* species B. The width of the paroccipital process decreases gradually towards the extremity of the process, however, the process remains a massive and strong structure all over. The part lateral to the base of the paroccipital process is dorsoventrally flattened resulting in a elliptical cross-section. Thus, its posterior edge is developed as a faint ridge, named the posterior ridge of the paroccipital process here, that is connected with the ventral border of the supraoccipital shelf (Figs. 2.11, 2.17). It travels in the middle of its posterior face and finally merges with the posterior surface at mid-length of the process. In the lateral half, the height of the paroccipital process is significantly increased. This is achieved on the one hand by a dorsal expansion of the

process, according to SMNS 4378 largely a contribution of the squamosal (Fig. 2.6), which increasingly narrows the height of the posttemporal fenestra and forms the ventrolateral border of the opening. Dorsally, a deep groove is developed below the overhang of the parietal process of the squamosal that leads into the posttemporal fenestra (Figs. 2.11, 2.41). More conspicuous, however, is the contribution of a ventral ridge to the overall height of the paroccipital process. The base of the ridge is confluent with the occipital face, resulting in a high and vertical surface of the lateral half of the paroccipital process in posterior view. In some specimens, the ventral ridge terminates abruptly towards the medial part of the paroccipital process, which results in a angular appearance of the expanded part of the paroccipital process. Since the ventral ridge descends from the posterior edge of the paroccipital process, the anterior face is recessed ventrally forming a concavity towards the opisthotic-quadrate suture (Fig. 2.11). Thus, a horizontal shelf is developed, the anterior edge of which forms the sharp posterior border of the tympanic fossa (e.g. Fig. 2.44A). The deeply serrated suture between the opisthotic and the quadrate head runs anterolaterally on the edge of the shelf (Fig. 2.17). The extremity of the opisthotic is braced against the paroccipital process of the squamosal with its anterolateral face.

Basisphenoid. Only the ventral side of the basisphenoid is open to a description. In many, but not all specimens (e.g. BMNH 42743), there is a fontanella-like fissure along the mid-line of the corpus of the bone (Figs. 2.9, 2.16). The pterygoid processes are situated far forward on the corpus and point ventrally and somewhat anterolaterally (Fig. 2.25). They are short and stocky, and expand rapidly to form the round articulation with the pterygoid. The bases of the processes are connected to form a transverse, concave elevation on the corpus, which shows a sharp ridge on each side of the mid-line. Anterior to the elevation, a fossa runs toward the parasphenoid (Fig. 2.9). In SMNS 5726, a foramen is located in the fossa just behind the cultriform process (comp. *Nicrosaurus* sp. SMNS 12593, subsection 2.3.3). Posteriorly, the basisphenoid broadens and turns steeply downward to form both the crescent-shaped anterior halves of the basal tubera. This results in a deep transverse pit on the basisphenoid between the pterygoid processes and the tubera.

Parasphenoid. The parasphenoid is fused to the basisphenoid and extends forward in the mid-line of the skull as a narrow process, separating the interpterygoid vacuity in two halves (Figs. 2.16, 2.19). It is visible for only a short distance on the palate and in ventral view disappears under the pterygoids. In ventral view, the base of the bone bears a sharp keel. SMNS 5727 shows that the bone is actually a V-shaped trough that opens to the ocular cavity, but more details are not preserved.

2.2.4 The mandible of *Nicrosaurus kapffi*

The lower jaw of *Nicrosaurus kapffi* has been meticulously described by MEYER (1861), and his figures (pls. 46-47, pl. 34 figs. 1-6) are among the most detailed available for a phytosaur mandible. In the material at hand, many details of the articular part of the mandible and the internal mandibular fenestra are indeterminable because of intensive damage to the specimens.

2.2.4.1 The openings of the mandible

The external mandibular fenestra is a long and slender opening occupying the ventral half of the articular part of the mandible. It is surrounded by the surangular dorsally and posteriorly, and the angular ventrally. The dentary embraces the anterior part of the fenestra overlapping both bones (Fig. 2.26B).

The internal mandibular fenestra is a large opening in front of the craniomandibular joint that opens dorsally to receive the main adductor muscles (ANDERSON 1936). The lateral border is formed by the surangular. The prearticular-articular complex surrounds the opening posteriorly (the glenoid facet) and medially, while the splenial contributes little to the anterior border (Fig. 2.26A, C). Anteriorly, the fenestra opens into the large Meckelian canal, which leads far forward and is enclosed between the dentary and an excavation of the internal side of the splenial.

The accessory internal mandibular fenestra (the infra-Meckelian foramen of WALKER 1961, 1990) is a small opening below the anterior rim of the internal mandibular fenestra. The fenestra is frequently dumbbell-shaped by a prong of the splenial, and in all specimens the posterior extent is poorly defined. The dorsal, anterior, and ventral border is formed by the splenial, the prearticular contributing to the posterodorsal rim, and the posterior rim by the angular. The fenestra is thus completely sealed off from the internal mandibular fenestra (Fig. 2.26C).

2.2.4.2 Osteology of the mandible

Dentary. The anterior part of the dentary is laterally expanded to receive the three enlarged dentary fangs. In contrast to the tip of the rostrum, the mandibular rosette is not deflected, but thickened and thus strongly convex on the ventral side.

In combination with the splenials, the dentaries form a broad and long symphysis, which in *Nicrosaurus kapffi* makes up about 40% of the mandibular length (Table 2.2.2). The symphysis is essentially a flat plane that is elevated for some millimetres above the

alveolar rim to form a symphyseal platform. Posteriorly, the symphyseal platform is not indented and the posterolateral parts are not tilted upward to merge with the diverging mandibular rami, but the platform remains horizontal and terminates abruptly in a well rounded transverse rim (Fig. 2.26A). A large foramen enters the posterior wall of the symphysis here, leading into the symphyseal canal that supplied the anterior teeth with nerves and blood vessels (Fig. 2.26C). A paired foramen penetrates the splenials to the left and right below the entrance to the symphyseal canal.

The postsymphyseal ramus of the dentary is bifurcated posteriorly, and embraces the anterior part of the external mandibular fenestra. The suprafenestral process extends along the anterior half of the fenestra, but does not touch the opening, and terminates in a notched rim (Fig. 2.26B). The infrafenestral process is more slender and reaches only about one fifth of the length of the fenestra. Both processes cover the surangular and angular, which effectively surround the external mandibular fenestra.

On the lateral side, a continuous dentary groove is developed (Fig. 2.26B). In its anterior half, deep, slit-like and regularly spaced foramina penetrate the mandible. Below the symphysis, the groove is situated at the mid-height of the dentary. Because of the expanding mandible height, the groove gradually shifts onto the dorsal third of the mandible further back, but always retains the same distance to the alveolar rim. At the level of the end of the symphysis, the dentary groove begins to broaden and gradually gets shallower, and finally runs out over the terminal notch of the suprafenestral process of the dentary to terminate in front of a foramen in the surangular.

Splenial. In dorsal view, the splenials form more than one half (55%) of the mandibular symphysis. Here, the splenials separate from the tooth row at tooth position d(28), and both bones form an acute triangle that separates the left from the right dentary (Fig. 2.26A; MEYER 1861: pl. 47 fig. 2). On the free mandibular ramus, the splenial is closely applied to the dentary. The bone forms the inner wall of the alveoli, which is somewhat higher than the lateral rim of the mandible formed by the dentary. The thickness of the splenial diminishes continually from the end of the symphysis and at the end of the tooth row, the splenial is mere a thin lamella. It contacts the coronoid process of the surangular with its posterodorsal corner. On the lateral side, the splenial appears on the ventral rim of the mandible below the posterior third of the tooth row, bordered by the dentary dorsally and the angular posteriorly (Fig. 2.26B).

Surangular. The surangular is a thin, plate-like bone forming the entire lateral wall of the internal mandibular fenestra. Above the mid-point of the external mandibular fenestra, the surangular rises to a short coronoid process that reaches the same height as the convexity of its dorsal rim just in front of the glenoid facet. Below the coronoid

process, a canal penetrates the medial wall of the surangular and exits as a foramen that opens anteriorly just in extension of the dentary groove (Fig. 2.26C). A thin vertical lamella of the surangular in extension of the coronoid process is wedged between the splenial and the dentary. Thus, the lateral wall of the last three mandibular alveoli is actually formed by two bones, the anterior lamella of the surangular being medially overlapped and largely hidden from view by the extremity of the suprafenestral process of the dentary on the external side (Fig. 2.26A; see also type of *Belodon plieningeri*, subsection 4.2.2).

Above the posterior fourth of the external mandibular fenestra, a strong, laterally projecting crest is developed that extends posteriorly over almost the entire postfenestral part of the mandible (Fig. 2.26A, C). The fading crest meets a narrow ridge that runs vertically to the anterior ridge of the glenoid facet. The crest forms a broad, smooth shelf between the coronoid process and the glenoid surface of the surangular. Posterior to the external mandibular fenestra, are a number of blunt ridges radiating from the ventral base of the crest onto the lateral posteroventral surface of the ramus. Here, the surangular meets the angular in a deeply concave suture.

In posterior view, the surangular forms the lateral ridge of the triangular facet contacting the articular in a well developed suture (Fig. 2.26A; MEYER 1861: pl. 34 fig. 3) and continues on the lateral face of the retroarticular process to the extremity of the mandible.

Prearticular-articular complex. Situated on the medial side of the mandible, the prearticular is fused with the articular and both bones form an indistinguishable prearticular-articular complex. The complex is described here as a single unit. Laterally, the composite bone is paralleled by the surangular and both participate in forming the glenoid facet for the quadrate, the triangular postglenoidal facet, and the retroarticular process (Fig. 2.26B). Medially, the articular part of the complex is extended into the medial process and the postglenoidal process (Fig. 2.26C). Ventrally, the prearticular-articular complex borders the angular.

There is no conclusive evidence for the presence of a discrete coronoid on the anteroventral side of the internal mandibular fenestra, as found in *Smilosuchus* (CAMP 1930: figs. 41-42) and reconstructed by CHATTERJEE (1978) for "*Parasuchus*". A bony lamella of similar outline is present in the same position (BMNH 38036), but it is impossible to discriminate this lamella from the prearticular by a sutural connection. Likewise, SMNS 5730 and BMNH 42744 show a similar lamina that is extensively fractured in this area. The mandibles of *Nicrosaurus* species B (GPIT 261/011, BMNH 38038) offer no further information because the anteroventral rim of the internal mandibular fenestra is broken off. In accordance with HUENE (1911), I regard the bone

present in the area in question as part of the prearticular-articular complex. The shape of this lamella is narrow and crescentic, contacting the splenial all along its ventral rim and it almost reaches the coronoid process of the surangular anterodorsally (Fig. 2.26C). Thus, the prearticular-articular complex forms the entire deeply concave medial rim of the internal mandibular fenestra.

The glenoid facet is strongly expanded medially, being at least three times wider than long. The glenoid surface traverses perpendicular to the axis of the mandible, in contrast to *Nicrosaurus* species B in which the glenoid facet is directed medially, but also somewhat forward (GPIT 261/011). The joint surface can be subdivided in two parts (Fig. 2.26A): the surangular contribution to the facet is narrow (about one fifth of the total width) and aligned with the dorsal rim of the surangular. This part of the glenoid is characterised by a gentle convexity from medial to lateral with a flattened apical surface, rather than being concave, and by a position on a higher level than the contribution of the articular to the joint surface. Anterior and posterior, the surangular contribution is drawn out into short, stout ridges forming the highest points of the glenoid facet. These ridges combined with the convexity result in a saddle-shaped form of the lateral section of the glenoid facet. The contribution of the articular to the glenoid facet forms a large, medially directed trough bound by two thin transverse ridges anteriorly and posteriorly. The trough is situated behind the internal mandibular fenestra, and its medial part projects over the medial face of the mandibular ramus. While the lateral side of the trough is bordered by the saddle-shaped surangular contribution, the facet is fully open medially without an elevated demarcation.

The medial process is basically a ventral extension of the glenoid facet, forming a large plate that is directed anteromedially at an angle to the medial face of the mandibular ramus (Fig. 2.26C). The dorsal face of the process is actually the concave medial extremity of the glenoid surface, being triangular in shape in dorsal view and greatly thickened transversally. The anterior corner of the plate-like ventral part of the process is extended to a blunt, anteriorly pointing prong. The plate merges posteriorly with the retroarticular process in the shape of a ridge that forms the medial edge of the triangular postglenoidal facet. Thus, the lateral process and the internal face of the mandibular ramus enclose a deep recess within the prearticular-articular complex that opens anteriorly and ventrally and is roofed by the medial part of the craniomandibular joint.

The delicate postglenoidal process, belonging to the articular, is only preserved in SMNS uncat. no. 9 (Fig. 2.26A, C). The process projects dorsomedially from the upper medial corner of the triangular facet. It is a broadly triangular plate with a transversely oriented base, the apex of which reaches the level of the articular part of the glenoid. Thus, the postglenoidal process and the posteromedial face of craniomandibular joint enclose a deep groove or recess that opens ventromedially.

In posterior aspect, the articular forms much of the triangular postglenoid facet, which was identified as the insertion area of the fleshy parts of the M. depressor mandibulae (ANDERSON 1936). The facet faces posterodorsally and is actually bipartite. It consists of a large central depression framed by a high, sharp ridge laterally, a contribution of the surangular (Fig. 2.26A), and a broader ridge medially that is extended to form the triangular process. A shallow depression is situated in the surangular between the lateral ridge and the articular-surangular suture. A third oblong depression is enclosed between the medial ridge and the ridge linking the medial process with the retroarticular process. The postglenoid facet tapers posteriorly to a triangular shape and grades into a short retroarticular process, most likely the insertion of a tendon of the M. depressor mandibulae (ANDERSON 1936).

The suture of the prearticular-articular complex with the angular runs almost horizontally from the base of the retroarticular process to the posterior tip of the accessory internal mandibular fenestra (SMNS 5730: Fig. 2.26C).

Angular. The angular is separated from the medial rim of the internal mandibular fenestra by the prearticular-articular complex, but forms the bottom of this large muscle chamber. The bone thus resembles a trough that opens dorsally (SMNS uncat. no. 9). The internal face is concave because of an increase in thickness of the angular dorsally towards the glenoid facet, which in BMNH 42744 is further enhanced by a medial deflection of its ventral rim. This creates a large recess enclosed by the medial face of the angular and the medial process of the articular. In the lowermost area of the recess, a long ridge parallels the ventral rim of the angular trailing towards the retroarticular process. In lateral view (Fig. 2.26B), the angular borders the external mandibular fenestra forming a rounded bar with a corrugated surface, the anterior part of which is hidden from view by the infrafenestral process of the dentary. The ridges and rugosities on the surangular continue onto the entire postfenestral face of the angular, and are also present on the entire infrafenestral process of the bone. Somewhat posterior to the level of the coronoid process, a knob-like protuberance of the fenestral rim of the angular projects dorsally into the external mandibular fenestra (SMNS 4380; SMNS uncat. no. 9). In front of the fenestra, the bone disappears between the dentary and the splenial.

2.2.5 The dentition of *Nicrosaurus kapffi*

With some notable exceptions (CASE 1924, 1930; MEHL 1928a), the exact morphology of the dental apparatus in a phytosaur taxon has so far received little attention. The dental descriptions available often include only selected, well-preserved teeth, which are considered "typical" representatives of the dentition (e.g. CAMP 1930: pl. 1). However, more frequently, generalised statements on the nature of the dentition are presented, sometimes with highly ambiguous terminology (e.g. "somewhat lancet-shaped", GREGORY 1962b: 11; "dagger-like teeth", LONG & MURRY 1995: 57). Isolated phytosaur teeth have usually been described and figured in much more detail (BUFFETAUT *et al.* 1988; CASE 1932b; CUNY *et al.* 1995; GODEFROIT & CUNY 1997; GUTH 1963; HUENE 1915, 1922; MCGREGOR 1906; MEHL 1913; MEYER 1861; SINCLAIR 1918). Such descriptions are hardly useful for the study of dental variation or for taxonomic purposes, because such specimens cannot be referred with certainty to any particular taxon.

The negligence of studies of the dentition in the current literature may be attributed to two reasons: Firstly, complete, *in-situ* dentitions of individual phytosaurs are generally rarely preserved, and direct evidence for tooth morphology in several taxa is not available (see Table 2.2.8). Secondly, MEYER (1861; 1865b) already realised, after studying the first well preserved phytosaur assemblage, that there is a confusingly diverse tooth morphology even among individuals, i.e., that phytosaur taxa exhibit a strong degree of heterodonty. As a consequence, dental characters played only a minor role in recent taxonomic and phylogenetic studies of phytosaurs (BALLEW 1989; GREGORY 1962b; LONG & MURRY 1995), or have been rejected altogether as being useless for this purpose (WESTPHAL 1976). However, this verdict seems somewhat premature. The dental characters of phytosaurs and the pattern of variation in the dentition have never been studied in detail. As long as positional (and probably ontogenetic) variation have not been separated from potentially valuable taxonomic information, there is the possibility that existing and useful evidence has been overlooked.

Here, for the first time, the complete upper dentition of a phytosaur is described in detail, based on *in-situ* teeth of two specimens, and the various tooth types are illustrated. The main aim is to identify and demonstrate the positional variation of dental features. This represents the first step towards a more objective definition of the degree of heterodonty in phytosaurs, and exploration of the potential of dental characters in phytosaur taxonomy.

2.2.5.1. Material and methods

The skull SMNS 5727 (Figs. 2.20, 2.27) and the snout fragment SMNS 13078 (Fig. 2.27) exhibit an almost complete dentition and form the basis of the description. In contrast to the majority of isolated phytosaur teeth from the Stubensandstein, however, *in-situ* teeth of *Nicrosaurus kapffi* turned out to be comparatively poorly preserved when examined under magnification. In particular, details of the serration (serration density and the shape of the denticles) proved difficult to document because of the effects of wear during the lifetime of the animal, and also because of damage to the delicate carinae by preparation. Such alterations by wear include progressive degrees of rounding of the denticles, thereby obscuring details, and inadequate preparation that resulted in partial or even entire annihilation of the carina ornamentation. For this reason, only a limited number of serration measurements could be taken, but it is assumed that these are typical for the teeth positioned in the immediately adjacent section of the jaw. Selected close-ups of denticles from well-preserved specimens are given when appropriate.

In the remaining specimens, few original teeth are preserved. In some specimens, (notably in the skull SMNS 5726 and the mandible SMNS 4380), many details have been obscured by restoration of parts of the teeth in resin, and frequently artificial teeth were put in place for display purposes. Although numerous teeth are present, the dentitions of the mandibles BMNH 38036 and BMNH 42744 are poorly preserved. For these reasons, the data provided by these specimens are restricted to tooth counts, and the mandibular dentition has to be treated in more general terms.

The following dental characters were studied:

- tooth crown height (TCH): the length of a line drawn from the tip of the crown to the basalmost extent of the enamel.
- fore-aft basal length (FABL): the distance between the mesial and distal face at the basalmost point of the enamel.
- basal width (BW): the labiolingual distance at the basalmost point of the enamel.
- overall shape of the tooth (illustrated by means of cross-sections in Figure 2.28 to Figure 2.38, and quantified by the ratio of FABL to BW).
- orientation of the tooth axis, subdivided according to the direction of the inclination into recurvedness (distal) and curvature (lingual).
- presence of carinae, and the length of the carinae relative to tooth crown height.
- presence of mesiodistally expanded carinae (flanges).
- position of the carinae on the tooth. Note that all directions given are relative to jaw geometry: the mesial side faces anteriorly, the distal side posteriorly. This does not

necessarily correspond to the orientation of isolated teeth, which are usually placed with the carina(e) in an anteroposterior plane thus defining the mesial and distal direction, the labiolingual axis being perpendicular to this plane.

- serration density (SD): measured in numbers of denticles per mm, and if not stated otherwise taken from the mid-section of the carina.
- shape of the denticles and interdenticle grooves.
- ornamentation of the enamel (striation, fluting, grooves, ridges, etc.).
- number of tooth positions.

2.2.5.2 Description

The nature of the dentition

The dentition of *Nicrosaurus kapffi* consists of a number of morphologically separated arrays of teeth in the upper and lower jaws, here introduced and described separately as dental sets. Five distinct dental sets are recognised: in the cranium the tip-of-snout set, the premaxilla set, and the maxilla set (Fig. 2.27). Consequently, the upper dentition of *Nicrosaurus kapffi* can be characterised as being tripartite. In the mandible, there is an additional tip-of-mandible set and a dentary set. Each of these dental sets can be defined by:

1. a distinct pattern of linear, non-reversible and usually gradual changes in a number of dental characters. In all dental sets, except the tip-of-snout set and the tip-of-mandible set, tooth morphology always begins with simple, undifferentiated teeth and leads, in each set, to characteristic, derived final members of the morphocline.
2. the relative position of each set in the jaw.

The identification of dental sets facilitates more systematical and more accurate documentation of changes in tooth morphology, demonstrates the polarity of transformations in each character (Tables 2.2.5 - 2.2.7), and, finally, helps to understand the dental sets as functionally adapted subunits of the dentition.

The tip-of-snout set

The tip-of-snout set includes four teeth only: two enlarged fangs pm (1) and pm (2), set in a rosette, the laterally expanded and downturned part of the snout, and two teeth situated in the anterior constriction (Fig. 2.27). The set is spatially separated from

the following premaxillary teeth by a diastema. In contrast to members of the other sets, the enamel of teeth in the tip-of-snout set never shows ornamentation and, because of the low number of teeth, character changes appear to be discontinuous.

The first two premaxillary teeth (Fig. 2.28) are the largest teeth in the dentition (tooth crown height reaches 55 mm in SMNS 13078, and 50 mm in SMNS 5727). In all specimens of *Nicrosaurus kapffi* in which the first two premaxillary teeth have been preserved, only one of them is fully erupted, whereas the second is in the process of being replaced, or the alveolus is occupied by a replacement tooth, which must be considered too small to be useful in a functional sense. Thus, the mode of replacement guarantees the functional integrity of the stabbing dentition at any time in life. The base of the crown is subrounded, only the lingual side being very gently flattened. The shape changes gradually to an oval diameter towards the apex (Fig. 2.28C), but the lingual face remains distinctly convex at any point of the crown. The straight distal edge of the tooth crown combined with a constantly curved mesial edge leads to a slight recurvedness of the whole crown.

The distal edge of the tooth crown forms a prominent blade-like rim over the whole height of the crown that lies in a sagittal plane relative to the jaw margins (Fig. 2.28C). The blade is separated from the body of the tooth by a longitudinal groove, a morphology which is regarded here as defining the flange of a tooth. The average serration density along the blade measures 4.5 denticles per mm (Fig. 2.28B). The denticles are subrectangular, twice as long as high and separated from the flange by a sinuous shallow furrow. The interdentical grooves cross the furrow and extend onto the flange where they fade out gradually (Fig. 2.28B). On the mesial side, a weaker, but fully serrated carina set at an angle of about 20° to the medial side runs over the apical two fifth of the crown. A peculiar case, possibly a pathologic condition, is found in the middle part of the right premaxillary tooth (2) of SMNS 13078, in which the distal carina is paralleled for some distance and finally substituted by a second carina placed more labially. This results in a doubled carina over three fifth of the tooth crown.. An example of a similar development of a carinate tooth edge in a phytosaur is represented by an isolated tooth figured in MEYER (1861: pl. 37 fig. 21). This is a feature not infrequently found among the carinate teeth of theropod dinosaurs as well. The potential origin of split or doubled carinae is further discussed in ERICKSON (1995).

The two succeeding teeth of the set are located in the constricted part of the snout following the expanded rosette. Here, tooth crown height decreases abruptly to about 20 mm and tooth shape becomes less differentiated. The third premaxillary tooth (Fig. 2.29) shows a marked bilateral asymmetry, the posteromedial side being strongly flattened, and displays two serrated carinae directed posterolaterally and anteromedially. In general

morphology, pm (3) resembles posterior premaxillary teeth such as pm (17). Pm (4) is round in cross-section, and the tooth axis is straight, with only the tip bent lingually (Fig. 2.30). Pm (4) shows only one weak and unserrated carina on the mesial face. The recurvedness seen in the fangs is not present in both teeth. The most characteristic feature in the posterior tip-of-snout set teeth is a change in tooth orientation: both teeth are wider spaced than pm (2), and to each other, than any other tooth of the entire dentition, and they represent the only teeth which point more laterally and posteriorly than ventrally. Pm (4) is set high up on the lateral side of the snout rather than being situated in line with the palatal surface, and points lateroventrally.

The premaxilla set

The premaxilla set of *Nicrosaurus kapffi* comprises between 12 and 20 tooth positions (Tab. 2.2.3) in all specimens under study. The teeth of the premaxilla set show a number of features that do not vary along the entire succession. Firstly, these teeth are

Table 2.2.3: Number of tooth positions in the cranium of *Nicrosaurus kapffi* (MEYER, 1860).

specimen	total length (in mm)	n tip-of-snout (left/right)	n pm (left/right)	n m (left/right)	total (left/right)	remarks
SMNS 54708	indet.	4	indet.	–	indet.	–
SMNS 4060	indet.	? / 4	?13 / 14	indet.	indet.	–
SMNS 4378	750	? / 4	16	18 / 19	?38 / 39	–
SMNS 4379	730	4	14	16 / 18	34 / 36	right maxilla: 1 alveolus secondarily closed
SMNS 5725	920 (est.)	4	14 / 12	16 /17	34 / 33	no marked post-tip diastema
SMNS 5726	775	3 / 3 1 / 1	15 / 14	18 / 19	37	diastema between pm(3) and pm(4)
SMNS 5727	765	? / 4	?21 / 20	19 /21	?44 / 45	left pm(1)-?(8), m(5)-(6), (11)-(13) reconstructed
SMNS 13078	900 (est.)	5 / 4	16	indet.	indet.	–
BMNH 42743	730 (est.)	4	14 / 15	20 / ?22	38 / ?41	–

Abbrev.: est. = estimated; indet. = indeterminate; ? = number estimated because of obscured alveoli.

not recurved or only incipiently so, and secondly, no marked mesiodistal asymmetry can be found in premaxillary teeth. This is also expressed in the values for fore-aft basal length which equal those for the basal width in all recorded tooth positions in the premaxillae. Lastly, there is only a slight increase in absolute height of the teeth, as expressed by values of 27 mm and 32 mm for the tallest anterior and posterior member of the premaxilla set in SMNS 5727. The apparent size differences between anterior and posterior premaxillary teeth in this specimen (Fig. 2.20) is a result of the pattern of the tooth replacement.

The anterior teeth of the premaxilla set are closely spaced. The crowns are almost bilaterally symmetrical with cross-sections grading from subcircular at the base of the crown to oval near the apex. The basal width is thus greater than the fore-aft basal length, and the width becomes proportionally larger towards the apex (Fig. 2.31C). In the anteriormost teeth, i. e. pm (5) to pm (8), the crowns are strongly arched inwards, and for this reason, the snout and the teeth form here a cage-like unity with a half-cylindrical shape. Tooth axes become more and more straight further back along the premaxilla. Pm (5) shows only one distal unserrated carina on the upper third of crown. Bicarination in the premaxilla set starts already with the next tooth pm (6), which shows two thin carinae over the apical half of the crown (Fig. 2.31A, B). The carinae lengthen progressively in the following teeth, however, the mesial keel always remains shorter than the distal carina. There are no flanges present. In anterior premaxillary teeth, only the apical part of each carina is serrated. However, the absolute length of the serrated part increases further back in correspondence with the length of the carinae. Details of the serration are not available. Up to pm (11), teeth of this set are ornamented with longitudinal, rather widely spaced striations on the apical half of the crown. These striae seem to be confined to the enamel, and appear as a faint staining rather than ridges, and show no distinguishable relief on the surface of the tooth crown.

In the middle of the premaxilla set (Fig. 2.32), starting at about pm (10), the lingual side of the crown becomes progressively more flattened towards the apex while the basal cross-section remains rounded or broadly oval. There is still a slight inward curvature of the tooth crown observable, but the continuous arching of the crown is gradually substituted by an angled, kink-like alignment of the crown with the root to the lingual side (Fig. 2.32C). This leads to significantly broader, almost rectangular alveoli that are centred more towards the alveolar ridge of the premaxilla than in anterior premaxillary teeth. The edge of the premaxilla projects ventrally forming gutter-like fittings to strengthen the anchoring of the roots (e.g. Fig. 2.33B-C; MEYER 1861: pl. 37 fig. 14). This can be first observed in pm (14) and finds its strongest expression in the last premaxillary teeth. The distinct shape of a posterior premaxillary alveolus might be used to identify the presence of such tooth types in specimens in which the actual dentition is

not preserved. The mesial and distal carinae show a further increase in length until in pm (13) both finally reach the base of the crown. This tooth also shows the first trace of a small flange-like expansion, basally, at the mesial side of the tooth crown. A distal flange occurs first in pm (14) (Fig. 2.32B). In the middle and posterior premaxillary teeth of SMNS 13078, the serration was found to be inconsistent. The carinae are fully serrated in pm (13). In the middle premaxillary teeth, the serration density shows the maximum value for the whole dentition with 6 denticles per mm. In the following tooth of SMNS 13078, however, the anterior carina is unserrated.

The terminal members of the premaxilla set (Figs. 2.33, 2.34) are the tallest post-fang teeth in the upper dentition, the ratio of tooth crown height to fore-aft basal length equalling 2.35 to 2.45 for pm (17) to pm (20). In overall appearance, all posterior premaxillary teeth are particularly slender because of the somewhat greater height of individual teeth in combination with a ratio of fore-aft basal length to basal width that remains constant in the tooth succession. The tooth axis is straight, though, in fully preserved dentitions the posteriormost teeth of the premaxilla set appear to be recurved because of a posteriorly inclined position in their alveoli (Fig. 2.34A). The entire crown of posterior premaxillary teeth is strongly bilateral asymmetric. The labial side is much more vaulted than in other tooth types, while the trend towards decreasing convexity of the lingual side, which is already expressed to some degree in the more anteriorly placed premaxillary teeth, reaches its maximum in an overall flattening. This results in an approximately D-shaped cross-section for posteriormost premaxillary teeth (Fig. 2.34C). The distal carina lies approximately in the medial plane of the tooth parallel to the jaw margin, whereas the mesial carina is always positioned lingual to the medial plane. Two lines drawn through the carinae and the centre of the tooth crown thus enclose an obtuse angle, which opens to the lingual side. In lingual view, the carinae and flanges are set off against the body of the crown and the flanges become progressively better developed in more posterior tooth positions of the premaxilla. In the posteriormost teeth, the flange extends over most of the crown (Fig. 2.34B, C). Both carinae are usually fully serrated, however, in at least one specimen, pm (20) of SMNS 13078, the serration gradually fades out at mid-height of the crown. The values for serration density are much lower than in more anteriorly positioned premaxillary teeth, with 2.5 denticles per mm in pm (17).

The maxilla set

The number of the teeth in the maxilla set varies from 16 to more than 20 teeth (Tab. 2.2.3). All maxillary teeth share the two following characters states that obviously

do not vary positionally: a constant small degree of curvature to the lingual side, and constant values for tooth crown height, which in fully erupted maxillary teeth of SMNS 5727 retain the figure of about 18 to 19 mm. The only exception, according to the size of the alveolus, is the much smaller posteriormost tooth of the maxilla (Fig. 2.27).

The anteriormost three maxillary teeth largely resemble anterior premaxillary teeth (Figs. 2.35, 2.36). However, they can be distinguished by their stouter appearance, their straighter, only slightly lingually curved tooth axis and their oval cross-section with mesiodistally oriented long axis at any point of the crown. A basal striation similar in appearance to that of anterior premaxillary teeth is present (Fig. 2.35A), but the ornamentation fades in more posterior positions, m (6) being the first tooth without striae. Flattening of the lingual side starts from the apex in m (4) and spreads within a few tooth positions over the whole crown, which leads to a D-shaped cross-section at about m (6) to m (8) as demonstrated in Figure 2.37. The labial side is more convex mesially than distally resulting in a mesiodistal asymmetry (Fig. 2.37C). The tip of the crown is always slightly recurved, but does not overhang the root because of the vertical orientation of the distal edge of the tooth in the jaw.

The development of carinae in maxillary teeth starts with an unserrated distal keel, present in m (1) to m (3) along one half of the crown (Figs. 2.35, 2.36). In m (6), the distal carina extends to the root and is fully serrated (Fig. 2.37C). In this tooth, the maximum value for serration density in the maxilla set is found, with 4 denticles per mm. In the same tooth position, a mesial carina can be observed for the first time in the set (Fig. 2.37C). It already extends over four fifths of the crown height, but only the apical half of the distal carina is serrated. At about position m (9), both carinae are completely developed and fully serrated. Beginning with m (4), a small distal flange can be seen developing in an apical position. In m (6), the flange runs over the whole distal edge of the tooth, and a mesial flange starts to develop from the apex. At about position (9), both edges show flanges along the entire tooth crown height resulting in the characteristically triangular outline of posterior maxillary teeth.

Maxillary teeth in an intermediate position, ranging from m (4) to m (8), are distinguished from somewhat similar posterior premaxillary teeth by the lower ratio of tooth crown height to fore-aft basal length, greater recurvature and the lack of fully developed blades (compare Figure 2.34 and Figure 2.37).

In the teeth posterior to m (9), the width of the flanges increases constantly, which accounts for a steady increase of the fore-aft basal length in posterior direction. The terminal members of the maxilla set (Fig. 2.38A, B) have a stout triangular appearance as a result of the fore-aft basal length being much greater than the basal width at any height

of the crown (TCH/FABL 1.05 to 1.15 in m (17) and m (18)). The crown is strongly bilateral asymmetric because of an increased flattening of the lingual side. Compared to anterior maxillary teeth, the vaulted labial side is also more convex mesially than distally (Fig. 2.38A). The tip of the crown is moderately recurved and overhangs the base of the crown (Fig. 2.38C). Tooth m (17) in SMNS 5727 is the only phytosaur tooth examined in this study that shows a wear facet located at the labial side of the tip.

In posterior maxillary teeth, two laterally expanded flanges extend over the whole height of the crown. The distal flange is broader and thinner, whereas the mesial flange shows a steeper slope towards the central vault of the crown (Fig. 2.38A). These characters contribute further to the marked mesiodistal asymmetry of posterior maxillary teeth. In lingual view, the flanges are separated from the body of the crown by two well distinguished furrows. Labially, the presence of well developed flanges results in both a prominent vaulting of the tooth body and a constriction at the base of crown. Towards the apex, the vault of the tooth body bears a vertical ridge paralleled by a broad and shallow longitudinal depression distally. The base of a mesial flange overlaps the preceding tooth at the labial side, which leads to the striking feature of a somewhat imbricate pattern of tooth arrangement only found in posterior teeth of the maxilla set (Fig. 2.38F). Thus, a continuous cutting edge is formed over the posterior part of the maxilla. Both flanges are convex and slightly S-shaped in apical view (Fig. 2.38C) and are set in a plain parallel to the axis of the jaw margin.

Posterior maxillary teeth are much more coarsely serrated than any one of the other teeth of the dentition: serration density equals on average 2.3 to 2.5 denticles per mm on both carinae. The denticles are of subquadratic shape, measuring, in m (17), 0.5 mm in length and 0.45 mm in height. They are separated by a deep notch leading into a straight interdentical groove that terminates abruptly (Fig. 2.38D). Apical denticles are smaller (0.35 to 0.4 mm long and 0.4 mm high) and less well separated (Fig. 2.38E).

The mandible of *Nicrosaurus kapffi* evidently contains a larger number of teeth than the upper jaw (Tab. 2.2.4; MEYER 1861: 295, pls. 46-47). In marked contrast to the upper jaw, these teeth are arranged in only two sets: a tip-of-mandible set located in occlusal position to the posterior teeth of the tip-of-snout set in the premaxilla, and a dentary set comprising the rest of the mandibular dentition.

Table 2.2.4: Number of tooth positions in the mandible of *Nicrosaurus kapffi* (MEYER, 1860).

specimen	total length (in mm)	n tip-of-mandible	n d (left/right)	total (left/right)	remarks
SMNS 4380	717	3	46	49	–
SMNS 5730	747	3	indet.	indet.	posterior part of dentary set fully obscured by matrix
BMNH 38036	715	3	?40 / ?42	?43 / ?45	alveoli of dentary set partially obscured by matrix
BMNH 42744	710	3	?36 / ?41	?39 / ?44	alveoli of dentary set partially obscured by matrix

Abbrev.: indet. = indeterminate; ? = number estimated.

The tip-of-mandible set

The tip-of-mandible set includes three enlarged fangs, of which, according to the size of the alveoli, the first one, d(1), is significantly smaller than the more laterally and posterolaterally placed second and third dentary teeth. A fragment of d(2) in BMNH 38036 resembles strongly pm(2) described above: the cross-section is round to oval with no significant transverse flattening, and a prominent posterior carina is present. There is no evidence of smaller and curved tip-of-mandible set members corresponding to the premaxillary teeth pm (3) and pm (4), and a well distinguished post-tip diastema is lacking. In occlusion, the third pair of dentary fangs slots into the post-tip diastema of the premaxilla: this is indicated by a more or less well established groove on the lateral side of the constricted area of the rostrum.

The dentary set

All dentary teeth posterior to the three enlarged fangs are smaller than their counterparts in the upper jaw. Most importantly, there is no enlargement of the dentary

teeth in occlusal position to the posterior premaxillary teeth. The anterior teeth of the dentary situated to about the end of the mandibular symphysis are small, round in cross-section, and striated at the base. In contrast to the striated teeth of the upper jaw, the ornamentation shows a comparatively prominent relief on the surface of the enamel. Such teeth contrast somewhat similar mandibular teeth of *Nicrosaurus* species B in being stouter and much more robust, and in tapering over the whole tooth crown length to a comparatively blunt apex. Posterior to the symphysis, there is a gradual change to unstriated, bicarinate, and lingually flattened teeth which generally resemble posterior maxillary teeth. The transition, however, is rather abrupt compared to the corresponding grade in the maxillary dentition, and takes place within a few tooth positions. By contrast to their antagonists in the maxilla, posterior dentary teeth have lower values for both tooth crown height and fore-aft basal length, and much narrower flanges. The tooth axes are straight, or the teeth are only very slightly recurved. The labial side of the posterior dentary teeth is also less vaulted than in their counterparts, which means that the crown is less asymmetric linguolabially. As in the maxilla, the posteriormost dentary teeth show an imbricating pattern of tooth arrangement and form a continuous row of teeth of essentially the same height. In the whole dentary set, no tooth shapes similar to posterior premaxillary teeth are present.

2.2.5.3 Positional variation in the jaw of *Nicrosaurus kapffi*

The variability in dental character states in *Nicrosaurus kapffi* described above forms a pattern of gradual changes. Most of the character states are correlated with the position of a tooth within a set, and thus with its location in the jaw. Such varying character states are therefore interpreted to represent positional variation. The main observations are presented graphically in Table 2.2.5 to Table 2.2.7. The following summary focuses on the sets in the premaxilla and maxilla.

It is noteworthy, that among all three dental sets present in the upper dentition of *Nicrosaurus kapffi* the same dental character states are included. There is always a labiolingual asymmetry of the teeth, and in all sets, the carinae, flanges, and denticles are present at least in some members. These characters may developed to a different degree (e.g. the density of serration and the degree of labiolingual flattening) along a dental set, but as far as can be determined there is no character qualitatively unique to a particular set. This suggests that only one morphogenetic programme is needed to create the morphologically different premaxilla and maxilla sets of *Nicrosaurus kapffi*, primarily by altering the parameters or the speed of changes that take place.

Table 2.2.5: Positional variation in the tip-of-snout set

Range: rosette and diastema of premaxilla
Number of teeth: 4

Tooth position (pm)	1	2	3	4
Tooth crown height	← marked decrease →			
Cross-section	lingually flattened	decrease of flattening lingually	oval →	
Mesial carina	← apical two thirds of crown →			
Distal carina	full height of crown	slight decrease in length →	not present	
Flange	expanded flange distally	decrease in width →	← no flange present →	
Serration of carinae	← fully serrated →		unserrated	
Recurveness (mesiodistally)	moderately recurved	straight →		
Curvature (labiolingually)	straight	tip strongly curved lingually →		
Orientation of tooth axis	ventrally	ventrolabially →		

Tooth size. With the well-known exception of the fangs in the tip-of-snout set, the maximum tooth crown height in a set does not change significantly (premaxilla set and tip-of-dentary set), and there is only a slight increase of size in the posterior positions of the maxilla set.

General morphology. The premaxilla and maxilla sets show a general trend towards bilateral asymmetry in the posterior tooth positions. This is achieved by a flattening of the apex on the lingual side, that spreads towards the base of the crown in posterior members of both arrays. Mesiodistal asymmetry is much more pronounced in the maxilla set. An increasingly stronger degree of the curvature in the mesial compared to the distal edge leads to a more and more recurved crown that finally overhangs the root. The distal part of the labial side becomes less vaulted than the mesial part, while its flange is more expanded laterally.

Carinae. The anteriormost teeth of a set are the least derived ones and show most affinities with simple conical teeth. This must be considered the character state from which differentiated teeth have evolved. However, in *Nicrosaurus kapffi*, even such underived teeth show at least traces of one distal carina. This might suggests that the possession of unicarinate teeth is a plesiomorphic feature of the species, if not of

Table 2.2.6: Positional variation in the premaxilla set

Range: diastema to posterior constriction of premaxilla
Number of teeth: 15-17

Tooth position (pm)	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Tooth crown height	increase →																
Cross-section	basal: circular apical: oval →			bilateral symmetry →				basal: oval apical: lingual side flattened →		bilateral asymmetry →				increase of flattening lingually →			
Mesial carina	not present →		apical third of crown →			increase in lenght →						full height of crown →					
Distal carina	apical fourth of crown →			increase in lenght →							full height of crown →						
Flange	← no flange present →								basal flange distally →		basal flange mesially →			increase in height →			
Serration of carinae	unserrated →			increasing length of serration →							fully serrated →						
Recurveness (mesiodistally)	← not recurved →												slight increase in recurveness →				
Curvature (labiolingually)	← strongly curved lingually												slightly curved lingually	to straight →			
Striation	← apical striation →												unstriated →				

Table 2.2.7: Positional variation in the maxilla set

Range: posterior constriction to end of maxillary
Number of teeth: 19-20

Tooth position (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Tooth crown height	← constant →																			
Cross-section	←oval→		increase of lingual flattening at apex →									increase of flattening lingually and mesiodistal asymmetry →								
Mesial carina	not present	rapid increase in length →						← full height of crown →												
Distal carina	apical half of crown	increase in length →						← full height of crown →												
Blade	no flange present	distal flange	mesial flange →									increase in width of flanges →								
Serration of carinae	unserrated	distal: fully serrated mesial: increase in length of serration →						← fully serrated →												
Recurveness (mesiodistally)	slightly →																		moderately →	
Curvature (labiolingually)	← slightly curved lingually →																			
Striation	fainting of basal striation →							← unstriated →												

phytosaurs in general. Unicarinate teeth are followed by a series of bicarinate teeth, in which the carinae spread progressively downwards along the edges, the mesial carina being somewhat shorter than the distal. From intermediate positions onwards, the teeth are fully bicarinate in both sets.

Serration. The length of the serrated part of the carinae develops generally in accordance with the length of the carinae. However, this character seems also to be subject to variation in individual teeth. There is evidence that the serration density varies strongly according to tooth position. In the anterior parts of the sets, the denticles are small and closely spaced (6 denticles per mm in the premaxilla set, 4 denticles per mm in the maxilla set). In these and intermediate positions of the maxilla set, there are also differences between mesial and distal serration density, the latter being finer. In the posterior members of both sets, the density is much coarser (2 - 2.5 denticles per mm) and the denticles are evenly distributed on both carinae.

Flanges. The increasing development of mesial and distal flanges is characteristic in particular of maxillary teeth and accounts for the marked disparity in fore-aft basal length and basal width. Flanges also develop in posterior premaxillary positions, but remain comparatively narrow and only clearly demarcated in lingual aspect. Both sets show opposite developmental traits regarding this character: the flanges of maxillary teeth first appear near the apex, whereas in premaxillary teeth, the flanges spread from the base apically. This is another reason that suggests that both sets are independent entities.

The predominance of positional character variation in the dentition of *Nicrosaurus kapffi* allows the assignment of isolated teeth to a specific position in the jaw, at least concerning the fangs and the terminal members of the premaxilla and maxilla sets. However, the less specialised tooth morphologies such as those found in the anterior parts of the premaxilla and maxilla sets, respectively, are virtually indistinguishable from each other. Since these tooth types also occur in other archosaurs (e.g. sphenosuchians), it is often impossible to identify such teeth with any certainty as phytosaurian when they are found isolated. A practical example listed in chapter 1 (Tab. 1.1) is represented by comparatively unspecialised teeth named *Termatosaurus albertii* by PLIENINGER in MEYER & PLIENINGER (1844). Originally not referred to a particular reptilian group, this tooth taxon has been identified as phytosaurian (FRAAS 1896), but also has been referred to sauropterygians (HENRY 1876; HUENE 1902; SAUVAGE 1907). In fact, the affinities of *Termatosaurus* are impossible to determine (BARDET & CUNY 1993; CUNY 1995).

2.2.5.4 Non-positional variation

Tooth positions. The number of tooth positions per premaxilla set and maxilla set is highly variable in *Nicrosaurus kapffi*, both within opposing tooth rows and among individuals (Tab. 2.2.3). Differences between the left and right side in an individual occur regularly, but never include more than three positions. Among the six individuals included in Table 2.2.5, the difference in maximum tooth count, however, amounts to eight tooth positions, representing approximately 20 % of the total tooth number in the species. No direct correlation between a decrease in the tooth count with increasing skull size is evident, although the large skull SMNS 5725 shows the lowest number of teeth (Table 2.2.3). Hence, there is no clear cut evidence that reduction of teeth is a linear ontogenetic trait. This suggests that failure to replace single teeth, combined with obliteration of alveoli with old age, which ultimately results in ontogenetic reduction of tooth positions, is not such a significant contributor to the variability than proposed elsewhere (MURRY 1986). The variability of the total tooth count in a sample of specimens belonging to a well-defined phytosaur species casts some doubts on the significant taxonomic potential of this character (COLBERT 1947; GREGORY 1962a; MURRY 1989), at least in closely related taxa. In contrast to the posterior segments of the dentition, the number of teeth in the tip-set is fairly constant (Tab. 2.2.3). The notable exception is SMNS 13078, in which the left side of the tip-set-teeth includes five tooth positions (Fig. 2.27). The presence of an additional tooth results in the loss of the post-tip diastema in the affected side of the snout. This shows that the tooth count may be subject to individual variation even in such a small dental set.

2.2.5.5 Discussion

Defining the degree of heterodonty

Despite all statements that tooth morphology is virtually useless for phytosaur alpha-taxonomy and phylogenetic interpretations, the degree of heterodonty has been frequently accepted for diagnosing higher categories, especially genera (CHATTERJEE 1978; GREGORY 1962b; LONG & MURRY 1995). However, approaches to defining the degree of heterodonty in phytosaurs is often flawed. Sometimes, incorrect observations have been copied again and again, such as the often quoted alleged homodonty of *Mystriosuchus planirostris* (see section 4.2) or a "weak" heterodonty in *Angistorhinus* (see MURRY 1989 for the contrary). A more serious problem is represented by ill-defined terms that are in usage including "subhomodont", "slightly", "moderately", and "strongly" heterodont, which are all open to subjective interpretation. This is well

Table 2.2.8: Classification of phytosaur taxa according to bipartite and tripartite upper dentitions.

bipartite upper dentition	tripartite upper dentition
based on the dental morphology	
"Parasuchus hislopi" *Paleorhinus parvus* *Rutiodon carolinensis* *Mystriosuchus planirostris*	*Leptosuchus adamanensis* *Leptosuchus crosbiensis* *Smilosuchus gregorii* *Nicrosaurus kapffi* *Arribasuchus buceros*
inferred from the size of the alveoli	
Francosuchus broilii *Ebrachosuchus neukami* *Paleorhinus bransoni* *Paleorhinus magnoculus* *Paleorhinus scurriensis* *Promystriosuchus ehlersi* *Angistorhinus grandis* *Angistorhinus talainti* *Brachysuchus megalodon* *Nicrosaurus* species B *Pseudopalatus pristinus* *Mystriosuchus* species B	none

illustrated by the dentition of *Nicrosaurus kapffi*, which has been assessed from being "not markedly heterodont" (LONG & MURRY 1995: 61) to showing the "highest differentiation" among phytosaurs (WESTPHAL 1976: 117).

Is there a possibility to distinguish between the degrees of dental differentiation more unambiguously? The definition of bipartite and tripartite dentitions in phytosaurs offers the basis for at least a primary dichotomous subdivision, which is easy to determine and much less subject to individual interpretation. The characteristics of a tripartite dentition in a phytosaur has been described in detail above. Bipartite upper dentitions include only the tip-of-snout set, and a large post-tip set encompassing the entire dentition behind the anterior constriction (see the descriptions of *Nicrosaurus* species B, and *Mystriosuchus planirostris*). This also finds an expression in the snout morphology: taxa characterised by a post-tip set do not show a significant enlargement of the posteriormost premaxillary teeth, and, consequently, there is never a ventral and lateral enlargement of the premaxillae in this region, and no trace of, or only an incipiently developed, posterior constriction at the premaxilla/maxilla border that is

typically present in specimens with tripartite dentitions. Based on these criteria, a classification of the upper dentition in phytosaurs is presented in Table 2.2.8.

Attributes such as "weakly", "moderately", and "strongly" heterodont imply the existence of a continuum from essentially uniform ("subhomodont") to highly differentiated ("strongly heterodont") tooth morphologies. This is not actually the case. Taxa previously considered subhomodont to slightly heterodont (e. g. *Nicrosaurus* species B) show only two dental sets: the tip-of-snout set and a large post-tip set. The tripartite dentition as expressed in *Nicrosaurus kapffi* cannot be regarded as an intensified version of a "weakly" heterodont form, which may be derived by a gradual increase of already expressed dental characters. Tripartite dentitions differ in the introduction of a whole new array of teeth, the premaxilla set, and include previously absent tooth morphologies. Such deep-founded dental disparities are unparalleled in modern reptiles. It is difficult to see how bipartite and tripartite dentitions can be developed within members of the same species, especially because bipartite and tripartite dentitions imply a substantially differing autecologic status (e.g. potential food spectrum, prey preference, habitat preference, position in food web). Provided the number of dental sets is genetically determined, the different nature of the dentition argues strongly for a genetic separation, and consequently for two distinct taxa, rather than an interpretation as one highly variable species. This reasoning is a strong argument for separating, for instance, *Nicrosaurus kapffi* from *Nicrosaurus* species B at the specific level.

At present, the available evidence of the morphology and variation of phytosaur dentitions allows no classification below the level of bipartite - tripartite dentitions, and no further redefinition of the various degrees of heterodonty, which have been used by other authors, is attempted here. However, there is evidence that suggests that a further subdivision might be possible according to the degree of transformation of dental characters within a dental set. The potential practicability can be illustrated by two examples.

The post-tip set included in the bipartite dentition of *Mystriosuchus planirostris* is characterised by a comparatively small number of differentiated maxillary teeth, usually confined to a grade covering the posteriormost six to eight tooth positions. Furthermore, these teeth differ in morphology (see subsection 3.2.2) to teeth in similar positions in other phytosaurs. In other bipartite taxa, the differentiation to triangular, trenchant tooth types starts more anteriorly, at about the mid-point of the post-tip set. *Mystriosuchus planirostris* is usually considered "homodont", although the same attribute has been used to characterise the more differentiated dentition of *Francosuchus* and *Paleorhinus* (CHATTERJEE 1978; GREGORY 1962a; WESTPHAL 1976). A redefinition of "homodont" based on the number of triangular teeth in the maxilla would result in more clarity.

Currently, the genus *Leptosuchus* is considered to include two valid species, *Leptosuchus adamanensis* and *Leptosuchus crosbiensis* (BALLEW 1989; LONG & MURRY 1995). However, it is difficult to refer specimens to species because of a morphological overlap between both taxa (LONG & MURRY 1995). Both taxa show tripartite dentitions. In *Leptosuchus adamanensis*, the posterior members of the premaxilla set are said to be enlarged relative to anterior premaxillary teeth, but the size differences are only slight (CAMP 1930: 36). A slight increase in tooth size is also seen in *Nicrosaurus kapffi*. By contrast, CAMP (1930: 44) describes the posteriormost premaxillary teeth in *Machaeroprosopus lithodendrorum* (junior synonym of *Leptosuchus crosbiensis*, LONG & MURRY 1995) as being "much enlarged", which is in accord with the situation in *Smilosuchus gregorii* and *Arribasuchus buceros* (see below). The relative size of the posterior teeth of the premaxilla set might prove appropriate for separating tripartite dentitions into two groups with increasing tooth differentiation.

Dental characters in phytosaur taxonomy

The teeth of *Nicrosaurus kapffi* show a number of dental characters that are differently developed in comparable positions in other phytosaur taxa. Therefore, it needs to be established how far such characters are restricted to less inclusive groups within Phytosauria. A discussion of the potential taxonomic variation in tooth morphology of phytosaurs on a more general level, and therefore an assessment of the taxonomic significance of phytosaur teeth, is seriously hampered by the lack of detailed studies of *in-situ* dentitions in other phytosaur taxa. In the course of this study, the teeth of the "less heterodont" *Nicrosaurus* species B (see subsection 2.3.3) and the least differentiated dentition in a phytosaur, represented by *Mystriosuchus planirostris* (see subsection 3.2.2), were examined in actual specimens. However, no detailed descriptions of other tripartite phytosaur dentitions are available, and comparisons are so far limited to scattered information of single individuals from the literature. For this reason, no satisfactory conclusions can be drawn, and the characters suggested below to be potentially significant for the taxonomy of species or higher categories must be regarded as tentative.

(1) The sections of the enlarged fangs of the premaxilla (pm (1) and pm (2)) are round to oval in *Angistorhinus grandis* (Mehl 1915), *Rutiodon carolinensis* (Colbert 1965), *Nicrosaurus* (Fig. 2.28), and *Mystriosuchus*. Among primitive phytosaurs, the shape of pm (2) in *Paleorhinus parvus* shows only a "slight lateral compression" (MEHL 1913: 148) in its apical section, which is in accordance with the taxa listed above. By contrast, BALLEW (1989: character 55) defined a character state "large, terminal fangs are

compressed" as a derived state of *Arribasuchus buceros*, and unique, at least, among her genus *Pseudopalatus* (here considered as *Pseudopalatus* and *Arribasuchus*). However, CAMP (1930: 58) noted that pm (1) and pm (2) of *Smilosuchus gregorii* are also lingually flattened, and he explicitly compared the shape of these teeth with an isolated, strongly bilaterally asymmetric tooth figured in HUENE (1921: fig. 2). Furthermore, a mandible referred to *Leptosuchus* bears a strongly asymmetric second dentary tooth, in which the lingual side achieves some degree of concavity (CASE 1924: fig. 10c-e). Since in *Nicrosaurus kapffi* the sections of the anterior three enlarged dentary teeth are subrounded (MEYER 1861: pl. 47 fig. 1) and thus correspond to pm (1) and (2), this may suggest that the enlarged teeth of the tip-of-snout set in *Leptosuchus* show the same asymmetry. Among taxa with tripartite dentitions, *Nicrosaurus kapffi* evidently differs from *Smilosuchus*, *Arribasuchus*, and possibly *Leptosuchus* in this character.

(2) Although teeth of the anterior premaxilla and maxilla set in *Nicrosaurus kapffi* are characterised by a faint striation, there is no tooth specimen included in the dental sets of the upper dentition that exhibits a prominent ornamentation of the enamel, i.e. an externally visible relief. No prominent tooth ornamentation has been reported in the tripartite upper dentitions of *Leptosuchus crosbiensis*, *Smilosuchus gregorii*, and *Arribasuchus buceros* either. This is in marked contrast to *Nicrosaurus* species B and both *Mystriosuchus* species, in which at least the anterior undifferentiated teeth of the post-tip set are fluted with a distinctive, coarse relief formed by both enamel and dentine (pers. obs.; comp. MEYER 1861: 310, pl. 37 fig. 1). A distinct fluting of the teeth in the upper dentition is found in the anterior teeth of *Paleorhinus parvus* (MEHL 1913), and in the anterior teeth of the premaxilla and maxilla set of *Leptosuchus adamanensis* (CAMP 1930: 58; pl. 1 fig. c). GREGORY (1962b) noted a comparable fluting of anterior premaxillary teeth of *Rutiodon carolinensis*, and a number of phytosaur taxa from the Newark Supergroup, usually regarded as junior synonyms of *Rutiodon carolinensis*, such as *Suchoprion aulacodus* (HUENE 1921: fig. 3) or *Suchoprion sulcidens* (HUENE 1921: fig. 5), are based on isolated phytosaur teeth showing the same feature. This distribution suggests, at first glance, that fluting of teeth in the upper dental sets is restricted to bipartite forms. However, it includes also the tripartite *Leptosuchus adamanensis*, and thus the lack of prominent tooth ornamentations at least in the upper dentition might be a character that could be used in a species diagnosis.

(3) The third tooth of the tip-of-snout set in the type of *Machaeroprosopus validus*, now lost, is said to have been greatly enlarged (MEHL 1916, 1922). This corresponds to *Arribasuchus buceros*, taken from the diagnosis of the junior synonym *Machaeroprosopus tenuis* in CAMP (1930: 50, 52) founded on a paratype specimen, and

reading "third tooth but a little bit smaller [than the two enlarged ones in the tip of the premaxilla] and well separated from fourth". In *Nicrosaurus kapffi*, and to my knowledge in all other phytosaurs, only the first two alveoli of the premaxilla bear the large fangs, pm (2) usually being the largest tooth of the upper jaw dentition. Pending on the correctness of the description of *Machaeroprosopus validus* and a more thorough determination of the size variation in contemporaneous specimens, both species exhibit a unique dental character state that is potentially autapomorphic.

(4) LONG & MURRY (1995: 57) noted the presence of "dagger-like teeth at *mid-length* of premaxilla" (my italics) in the diagnosis of *Arribasuchus buceros*. Interpreting "dagger-like" as not recurved, bicarinate and flattened labiolingually. This tooth morphology is not present in *Nicrosaurus kapffi*, and this term does clearly not apply to its teeth in mid-positions of the premaxilla set.

(5) The criteria of size in posteriormost premaxillary teeth has been suggested above to be not only potentially useful for defining the degree of heterodonty, but also for distinguishing between *Leptosuchus crosbiensis* and *Leptosuchus adamanensis*. *Smilosuchus gregorii* shows a considerable enlargement of the three posteriormost teeth in the premaxilla set (CAMP 1930: 90; COLBERT 1947). According to CAMP's reconstruction (CAMP 1930: fig. 11b), the size increase is apparently abrupt, resulting in a doubled tooth crown height compared to the immediately preceding tooth. Similarly, the posterior teeth in the premaxilla set of *Arribasuchus buceros* are much larger than any other tooth of the set (LONG & MURRY 1995). CAMP (1930: 52) gives the number of five (pm (14) to pm (18)) out of 19 premaxillary teeth. There is no information about the degree or mode of enlargement given, although CAMP (1930: fig. 11d) reconstructed a gradual increase in tooth crown height over several tooth positions. *Nicrosaurus kapffi* differs considerably from *Leptosuchus crosbiensis*, *Smilosuchus*, and *Arribasuchus* in showing only an insignificant size increase of the teeth across comparable positions.

(6) *Smilosuchus gregorii* shows a shortening of the premaxilla set by an incorporation of the last three premaxillary teeth into the maxilla set (CAMP 1930; COLBERT 1947). This corresponds to the definition "shift of maximum tooth size anteriorly for two positions", which has been suggested to be autapomorphic for *Smilosuchus gregorii* by BALLEW (1989: 323, character 31). The dentition of *Nicrosaurus kapffi*, by contrast, is usually characterised by the last premaxillary tooth being the largest member of the premaxilla set. However, it is remarkable that the extent of the premaxilla set in *Nicrosaurus kapffi* does not necessarily coincide with the length of the bone from which its name derives, but may cross the boundary to the next tooth-

bearing element. In the specimens SMNS 5725 (Fig. 2.13), SMNS 5727 (right side, Fig. 2.27), and SMNS 13078 (right side, Fig. 2.27), the last premaxillary tooth has to be included in the maxilla set, both according to its size and morphology. Nevertheless, there is never more than one "anterior maxilla tooth-type " in the posteriormost section of the premaxilla, corroborating the validity of BALLEW's character assessment. Furthermore, this indicates that the morphogenetic programmes which are responsible for the development of the dental sets are not selective for a particular bone, but rather apply to a particular distance on the dental lamina.

(7) An incomplete phytosaur skull from the Rhaetian of Salzgitter, which has been referred to the poorly known genus *Angistorhinopsis* (Tab. 1.1), shows a diastema of 40 mm (right side) and 50 mm (left side) in the posteriormost section of the premaxilla at the border with the maxilla (HUENE 1922: 124, fig. 130). The symmetry of the discontinuation suggests that this is not a pathologic condition, in contrast to asymmetric obliteration of alveoli (e.g. CAMP 1930: 44). A tooth-less space of this dimensions among the usually continuous tooth row of the rostrum has never been reported in any other phytosaur specimen.

2.2.6 The diagnostic characters of *Nicrosaurus kapffi*

2.2.6.1 Diagnostic characters

(1) presence of a continuous prenarial crest reaching just behind the downturned tip of the snout (LONG & MURRY 1995; BALLEW 1989: character 37, in parts); [absence of a crest, or a partial prenarial crest terminating at mid-point of the rostrum].

Smilosuchus gregorii is the only other phytosaur that appears to have a continuous prenarial crest (BALLEW 1989; LONG & MURRY 1995). This does not prevent *a priori* the diagnostic status of the character for *Nicrosaurus kapffi*. However, I feel that either unclear definitions, such as which features constitute a "fully crested" specimen, or the indiscrete nature of some individual crests contributed to some confusion (e.g. the assignment of partial and full crests to specimens in CAMP 1930, see BALLEW 1989: 311). This is particularly the case in *Smilosuchus*. BALLEW (1989) and LONG & MURRY (1995) noted, that the prenarial crest of the holotype is flattened by compaction. In other specimens (COLBERT 1947; LONG & MURRY 1995: fig. 29B) it is arbitrary to decide where, or if at all, the crest ends and merges into a "normally shaped" rostrum. A similar situation seems to be present in *Arribasuchus buceros*. BALLEW (1989: 331) lists in the diagnosis of this species that some specimens show a fully extended prenarial crest. The same species was characterised by LONG & MURRY (1995) as being partially crested only. The situation is unambiguous, and the length of the prenarial crest is a discrete character in *Nicrosaurus kapffi* because of autapomorphy (2) below.

(2) top of prenarial crest straight or slightly convex (LONG & MURRY 1995, in parts); [top of prenarial crest sloping downwards].

This character state is unique to *Nicrosaurus kapffi* and describes the crest shape that has been considered characteristic for the species since MEYER's (1861) monograph. *Smilosuchus gregorii* and almost all phytosaurs with partial prenarial crests show the primitive descending snout profile.

2.2.6.2 Potentially diagnostic characters in need of further substantiation

(3) posttemporal fenestra bound lateroventrally by an extension of the squamosal that rests on the occipital face of the paroccipital process; [posttemporal fenestra bound ventrally by the paroccipital process of the opisthotic].

The mode of lateral closure of the posttemporal fenestra by the squamosal as indicated by *Nicrosaurus kapffi* SMNS 4378, and not by the opisthotic, is uncommon, but not a unique feature among phytosaurs.

A partially similar situation to SMNS 4378 is evident in *Mystriosuchus* species B (HUENE 1911: fig. 7; this study, Fig. 3.5). In this specimen, a ventral extension of the base of the parietal process covers parts of the anterior face of the paroccipital process. However, there is no indication that the squamosal extends on the posterior face of the process and borders the posttemporal foramen ventrally. Nevertheless, the coincidence in at least one other taxon strengthens the likelihood that the reconstruction for *Nicrosaurus kapffi* is accurate at least for the anteriorly facing part of the squamosal extension, although this feature is only demonstrable in one specimen.

The squamosal bordering or embracing the lateral corner of the posttemporal fenestra can be seen in the reconstructions of *Pseudopalatus pristinus* (BALLEW 1989: fig. 2D; MEHL 1928b: fig. 4) and might have been present in *Machaeroprosopus validus* as well (MEHL 1916: fig. 3). A lamella of the squamosal, which is topologically in the same position and thus may correspond to the part of the squamosal forming the ventral sulcus in *Nicrosaurus kapffi* (Fig. 2.11), closes the large posttemporal fenestra of *Pseudopalatus* laterally. According to the illustration provided, the same is obviously achieved in the type of *Machaeroprosopus* by the paroccipital process of the bone.

An extensive squamosal-opisthotic contact that includes the ventral border of the posttemporal fenestra is paralleled only in *Angistorhinus grandis*. According to MEHL's (1913) reconstruction, a large plate-like process of the squamosal extends ventromedially to contact broadly the supraoccipital. A second, much shorter process runs downward and contacts the anterodorsal edge of the paroccipital process of the opisthotic. Both processes thus form the dorsal and the lateral part of the ventral border of a large posttemporal fenestra. Basically the same pattern is developed in *Angistorhinus talainti*, but the lateral descending process reaching the opisthotic is confluent with the paroccipital process of the squamosal and well apart from the posttemporal fenestra (DUTUIT 1977a).

However, the condition in *Angistorhinus*, *Pseudopalatus* and *Machaeroprosopus* is not comparable in detail to that in *Nicrosaurus kapffi*. In neither of these cases does the squamosal extend onto the posterior surface of the paroccipital process of the opisthotic. The condition in *Angistorhinus* is largely a result of the elongated and broadly overhanging squamosals, while the parieto-squamosal bar is still in the plesiomorphic dorsal position. The configuration in *Pseudopalatus* and *Machaeroprosopus* is actually caused by the peculiarity that in these specimens, unlike in *Nicrosaurus*, the paroccipital process is detached dorsolaterally from the parieto-squamosal bar. *Mystriosuchus* species

B comes very close to *Nicrosaurus kapffi*, but probably because of the tiny posttemporal fenestra in this genus, the squamosal fails to enter the ventral border for spatial reasons.

In conclusion, the configuration around the posttemporal fenestra of *Nicrosaurus kapffi* (SMNS 4378) is unmatched in other taxa. However, I think it is premature to postulate the extent of the squamosal onto the posterior face of the paroccipital process in connection with bordering the posttemporal fenestra ventrolaterally as a diagnostic character for the species, unless the state of this character can be confirmed in more specimens of *Nicrosaurus kapffi*.

2.2.6.3 Previously suggested autapomorphic characters, or characters that might be considered diagnostic

(i) ventrolateral flanges along the premaxillae (BALLEW 1989: character 36).

In contrast to the prominent flanges of the maxillae in the robust morphs of *Nicrosaurus kapffi*, lateral extensions of the premaxillae are sometimes present, but comparatively very poorly developed or incipient. An identification as such depends largely on the subjective judgement of an observer. In two specimens, flanges along the premaxillae are obviously absent (BMNH 42743: Fig. 2.22; SMNS 5727: Fig. 2.18) and the alveolar rim is similarly developed as in other phytosaur taxa. In the large specimen SMNS 5725, the development of premaxilla flanges seems to be associated with intensive superficial bone modifications of the snout.

(ii) greatest depth of prenarial crest at mid-length (LONG & MURRY 1995: 60).

Under the assumption that "depth" of the prenarial crest means dorsoventral extension, the character description is in conflict with one of LONG & MURRY's (1995: 60) other autapomorphies, which reads that the prenarial crest has a "straight dorsal profile". Factually, the statement holds true for SMNS 4378 and BMNH 42743 only, the high-domed and more gracile morphs of *Nicrosaurus kapffi*. In the low-domed morphs, there is no significant increase in crest height over its whole length.

(iii) top of prenarial crest rounded and never sharp (LONG & MURRY 1995: 60, "bulbousness" (?); BALLEW 1989: 326, "bulbous snout" (?)).

I assume that "bulbousness" refers to the shape of the crest top, although I find no prenarial crest particularly bulbous; with the exception of SMNS 5725, the flanks are always straight or concave. The character formulation of LONG & MURRY as quoted

above is correct for all specimens, although in SMNS 4060 and BMNH 42743 the morphology of the crest top is much narrower than in any other individual (Figs. 2.3C, 2.22). This is an inevitable consequence of the usual shape of the prenarial crest while combined with an extraordinarily narrow rostrum in these specimens. The morphology of the prenarial crest top in *Nicrosaurus kapffi* thus may approach the sharp-edged condition that is characteristic of *Arribasuchus buceros* (LONG & MURRY 1995), and that can be found in some specimens of *Nicrosaurus* species B as well (Tab. 2.3.3). However, the crest in *Nicrosaurus kapffi* is clearly not as knife-like as described for those taxa, and thus it is possible to define two distinguishable character states. The reason for not accepting "rounded top of prenarial crest" as autapomorphic is based on the polarity of the character states. Since the prenarial crest is a dorsal extension or an elevation of a plesiomorphically well rounded dorsal surface of the snout (see part 2.3.4.2), the rounded shape must be considered primitive not only for *Nicrosaurus kapffi*, but for any phytosaur taxon with a blunt crest top.

(iv) strong and low lateral flanges of the snout formed by the maxillae.

The lateral parts of the maxillae in the low-domed morphs of *Nicrosaurus kapffi* characteristically bulge laterally and form low, nearly horizontal maxilla flanges to the sides of the antorbital fenestrae. This is in marked contrast to all other phytosaur taxa with robust snouts, including those with particularly massive snouts, the brachyrostral type of HUNT (1989). In one specimen of *Smilosuchus gregorii*, the maxillae are high and vertical (COLBERT 1947), and in *Angistorhinus*, *Leptosuchus*, and the other specimens of *Smilosuchus* (CASE 1929; LONG & MURRY 1995: fig. 28A, 29), the maxillae are high, but only insignificantly expanded laterally in comparison with *Nicrosaurus kapffi*. However, in the high-domed morphs of *Nicrosaurus kapffi*, the laterally expanded flanges are absent (see variation, subsection 2.2.7), and the degree of lateral expansion is probably also subject to ontogenetic variation. Therefore, strongly splayed alveolar margins of the maxillae cannot be considered diagnostic for *Nicrosaurus kapffi*. The character is, if present in a specimen, nevertheless a character that distinguishes such specimens from other phytosaurs with massive snouts.

(v) the angular ("V-shaped") parietal-supraoccipital complex is less splayed and has steeper sides (BALLEW 1989: character 39).

BALLEW (1989) established this character as a derived state of *Nicrosaurus* (in her analysis, *Nicrosaurus kapffi*), which is claimed to be contrasted by *Rutiodon*, *Leptosuchus*, and *Smilosuchus*. Actually, the character is composed of two uncorrelated features of the squamosal processes of the parietals.

It proved impossible to quantify precisely the angle enclosed by the squamosal processes of the parietals on the basis of available data in all the named taxa, partially because of preservational reasons in single specimens, but also because of poor documentation in the literature. In *Nicrosaurus kapffi*, the angle enclosed between both squamosal processes varies between the extremes of 75° (SMNS 4378) and more than 110° (SMNS 4379). Similarly, the angle in specimens referred to *Rutiodon carolinensis* ranges from an estimated value of 80° (DOYLE & SUES 1995: fig. 1) to about 100° (GREGORY 1962b: fig. 6), only to be reconstructed as 120° (GREGORY 1962b: fig. 8). The observed wide range could be attributed to individual variation. On the other hand, the extreme low figure in SMNS 4378 suggests that the shape of the supraoccipital shelf, and therefore the angle of the squamosal processes, depends on the width of the skull, and hence it might be a dimorphic character in *Nicrosaurus kapffi*. Although two *Nicrosaurus* species B show a reduced "splayedness", this is also difficult to quantify and in this taxon correlated with an increased length of the supraoccipital shelf, which is not the case in other taxa with "reduced splayedness". In addition, it is obvious (from SMNS 5726 and SMNS 54706, for instance) that the delicate parietal laminae are prone to be affected by distortion. It is therefore concluded that this character is unsuitable for phylogenetic purposes.

It is not clear to me whether BALLEW's second character, the "steeper side" of the squamosal process, applies to the slope of the dorsal rim, meaning the shape of the medial part of the parieto-squamosal bar, or the orientation of the lamina itself, i. e. whether and to what extent the squamosal process of the parietal overhangs the supraoccipital shelf. Regarding the degree of slope of the dorsal rim, I do not see measurable differences between specimens of *Nicrosaurus*, *Leptosuchus*, and *Smilosuchus*. *Nicrosaurus* species B SMNS 12593 has clearly less steeply sloping rims than any of the aforementioned taxa. The inclination of the posterior surface of the process to form an overhang is easily subject to *post-mortem* deformation (see for example *Nicrosaurus* species B SMNS 12593, Fig. 2.48). In both features, there seem to be differences among phytosaurs, but no discrete character states are definable. The characters are not used taxonomically and phylogenetically in this study.

(vi) flattened posteromedial rim of posterior process of squamosal that faces medioventrally.

To my knowledge, this character state (Figs. 2.11, 2.41) has not been observed so far in any other phytosaur taxon and for this reason it would seem to have the potential of a diagnostic character for *Nicrosaurus kapffi*. However, a flattened area is definitely not present in the low-domed SMNS 5726. Instead the specimen shows the

plesiomorphically rounded rim, although markedly thickened as the squamosal rims of the other *Nicrosaurus kapffi*. The distribution of the character state presently allows us to refer specimens to *Nicrosaurus kapffi*, but it does not constitute a universally valid diagnostic character for the species.

(vii) broadly rounded posterior process of squamosal (BALLEW 1989: character 38, in part; MURRY 1989).

In dorsal view, the squamosal terminates in a rounded tip in all skulls referable to *Nicrosaurus kapffi*. The posteriormost extremity of the squamosal is never tapering or even pointed as in *Nicrosaurus* species B (with the limitation that the squamosal is known to date only from SMNS 12593), *Pseudopalatus* (MEHL 1928b; BALLEW 1989) and *Arribasuchus* (COPE 1881; LONG & MURRY 1995). According to the topologically more basally placed taxa of non-phytosaurid phytosaurs, *Angistorhinus*, and *Leptosuchus*, the rounded shape is the plesiomorphic character state within Phytosauria. Consequently, the rounded posterior process can not be listed as an autapomorphy (as I understand MURRY 1989) of an ingroup taxon, but only as a retained character state within a more derived clade. Additionally, there is the problem that the shape of the posterior process is not known in the high-domed morph of *Nicrosaurus kapffi*.

BALLEW (1989: character 38) apparently tried to avoid the polarity conflict by linking the shape of the squamosal tip with the low height ("compressed") of the squamosal body and the posterior process. Both character states, however, are plesiomorphic relative to *Nicrosaurus*, the first for the reason discussed above, the second even according to her own analysis (BALLEW 1989: character 12b). Hence, a combination of both character states cannot result in an autapomorphy of *Nicrosaurus kapffi*. Additionally, the combination of a round posterior process with a dorsoventrally high squamosal in *Angistorhinus* as opposed in *Nicrosaurus* (with dorsoventrally low squamosal) demonstrate, that a rounded posterior process and the height of the squamosal are two independent characters, which are not morphogenetically related. Therefore, they must be treated as separate characters.

2.2.7. Variation in the skull of *Nicrosaurus kapffi*

2.2.7.1 Description and distribution of variable cranial characters

The prenarial crest and the dorsal aspect of the rostrum

(1) degree of expansion of the snout tip

The tip of the snout is less laterally expanded in the skulls SMNS 4378, BMNH 42743, and the snout fragment SMNS 54708 (MEYER 1861: pl. 31 figs. 10-11). This character seems to be correlated with the less absolute snout width of these specimens (Tab. 2.2.1), and phytosaur taxa with slender snouts generally show less well developed snout tips.

(2) fusion of the anterior interpremaxillary suture

SMNS 5725 is one of the skulls in which the skull bones are especially well impregnated with diagenetically formed hematite along their sutures, and thus the course of a suture is readily followed by its deep red colour. The interpremaxillary suture is present on the top of the crest (Fig. 2.12, but partially obscured by the intensive sculpture over some distance) and most clearly at the extremity of the tip. SMNS 5725 is, however, the only specimen in which there is no trace of a median suture in the unsculptured and well exposed area of the anterior slope of the crest and the posterior part of the expanded tip of the snout, and the premaxillae seem to be fused here. In functional terms, bone fusion just in front of the crested and therefore rigid part of the snout must have resulted in additional resistance against strain and torsion in an area which was most likely to be exposed to bending stress caused by point loads on the expanded tip during a forceful bite.

(3) shape of the prenarial crest (see also part 2.2.4.3 (ii))

In the specimens SMNS 4060, SMNS 4378 and BMNH 42743, the top of the prenarial crest is markedly convex (Figs. 2.3B, 2.5C, 2.24). The apex of the convexity lies near a point at the mid-length of the snout. The other skulls of *Nicrosaurus kapffi* including the snouts SMNS 5725 and SMNS 13078 show an essentially straight top of the crest (e.g. SMNS 5725: Fig. 2.14) or slightly undulating crest (e.g. SMNS 5727:

Fig. 2.20) outline. The different types of prenarial crest shapes are illustrated in Figure 2.44B, E.

(4) width of the crest top (see also part 2.2.4.3 (iii))

SMNS 4378 shows a narrow dorsal rim of the prenarial crest (Figs. 2.5A, 2.44C). The lectotype SMNS 4060, though strongly damaged, must have had a similar narrow crest top (Fig. 2.3C). The extreme is seen in BMNH 42743 (Fig. 2.22), in which the crest top approaches the sharpness of the fully developed prenarial crest in *Nicrosaurus* species B. In SMNS 4379, SMNS 5726 and SMNS 5727, the anterior part of the crest is significantly broader than in all these specimens, and forms a more conspicuous, but still rounded angle with the flank (Fig. 2.44F). In SMNS 5727, the crest top is even somewhat laterally expanded resulting in an irregularly shaped ledge above the crest flanks (Fig. 2.20). The enormously enlarged crest width of the large skulls SMNS 5725 and SMNS 13078 is treated in the next character.

(5) half-cylindrical diameter of the crest

The maximum width of the prenarial crest in the large specimens SMNS 5725 and 13078 is significantly increased to more than double the width compared to the other specimens of *Nicrosaurus kapffi*, although SMNS 13078 is somewhat distorted and laterally compressed. A cross-section through the anterior part of the crest of SMNS 5725 would result in a semi-circular outline of the crest section (Fig. 2.12). The broadening shape of the crest results in an almost vertical orientation of the premaxillae at the base of the crest, in contrast to the sloping premaxillae in all other specimens. As another consequence, the infranasal recess along the naso-maxilla suture that demarcates the crest from the horizontal flange of the maxilla is particularly well developed in SMNS 5725 (Fig. 2.14). Furthermore, the width of the snout and the spoon-like extension of the tip is also significantly enlarged relative to smaller specimens (Tab. 2.2.1). There are neither differences in the height of the crest relative to the skull roof nor in the longitudinal profile of the crest, both of which are identified here as sex-dependent dimorph characters. It should also be noted that the posterior part of the crest of SMNS 5725 directly in front of the nares is not substantially inflated but retains its typical narrow profile in dorsal view (Fig. 2.12).

(6) steepness of the crest flanks

In SMNS 4060, SMNS 4378 and BMNH 42743, the flanks of the prenarial crest are steeper compared to the remaining specimens and approach verticality. The same

character state is present in the paralectotype snout fragment SMNS 54708 (Fig. 2.4). In all these specimens, the orientation of the crest flanks results in the narrower crest top. The steep crest flanks are associated with a more slender snout in these specimens. The different character states are illustrated in the cross-section of the snout SMNS 4378 (MEYER 1863: pl. 42 fig. 5) and BMNH 42743 (Fig. 2.44C), contrasted by SMNS 5727 (Fig. 2.44F).

(7) sculpture on the flank of the crest

In the steep prenarial crests, the almost vertical flanks are dominated by shallow vertical grooves that separate numerous low ridges. The surface of the crest has a undulating appearance and somewhat resembles corrugated iron (e.g. SMNS 4378, Fig. 2.5C). Although the same type of sculpture is also present in the morphs with more robust crests, it is far less conspicuously developed.

(8) width of the snout

The width of the snout is best expressed at readily determinable points, the first and second constrictions. The values for the first constriction of SMNS 4060 (35 mm) and SMNS 54708 (34.8 mm) is much below the figures seen in the other specimens (Tab. 2.2.1), although the snout of SMNS 4060 does not differ significantly in average width in the posterior premaxillary and maxillary section. SMNS 4378 shows a somewhat narrower snout than SMNS 4379, SMNS 5725, SMNS 5727, and SMNS 13078, but the narrow appearance of the rostrum in this specimen is greatly enhanced by the steep and high prenarial crest (Fig. 2.5). An extremely slender snout is present in BMNH 42743, the absolute values falling in the range of snout widths seen in *Nicrosaurus* species B (Tabs. 2.2.1, 2.3.1).

(9) intensive superficial bone remodelling of the prenarial crest

The dorsal surface of the snout in SMNS 5725, especially the surface of the crest, was in life obviously subject to intensive bone remodelling. The surfaces of the premaxilla and the maxilla, and to a lesser extent those of the nasal and septomaxilla, are dotted with minute holes, which results in a spongy superficial appearance of these bones (Fig. 2.12). The jaw margins of both premaxillae and maxillae show long, knobby protuberances which project laterally (Fig. 2.14), individuals of a unique pattern among *Nicrosaurus kapffi*. Additionally, the rugosities on the top of the crest are markedly increased in SMNS 5725, and bear irregularly shaped, up to 20 mm deep pits bounded

by sharp ridges. Similar sharp knobs are present on the anterior part of the prenarial crest of SMNS 4378 (Fig. 2.5A).

(10) steepness of the lateral face of the maxilla (presence of a maxillary flange)

The greatly flared maxillae of SMNS 4379, SMNS 5726, SMNS 5727 (Figs. 2.8, 2.15, 2.18), and especially SMNS 5725 (Fig. 2.12) form conspicuously jutted maxillary flanges below the antorbital fenestrae. Such maxillary flanges are much less developed in SMNS 4378 (Fig. 2.5A), and are entirely absent in BMNH 42743, in which the subfenestral part of the maxilla is almost vertical (Fig. 2.24).

(11) increased flaring of the maxilla

In SMNS 5725, the maxillae are much more expanded laterally than in the other specimens, as expressed in the measurements 11 and 12 in Table 2.2.1. The maxillae thus form a substantially larger and now horizontal shelf in the posterior part of the snout. As another consequence of the expansion, the antorbital fenestra no longer opens dorsolaterally, but only dorsally (Fig. 2.12).

(12) length and shape of the septomaxilla (Fig. 2.23)

The length of the anterior part of the septomaxillae in front of the nares is dimorphic in *Nicrosaurus kapffi*, and the length correlates with a particular shape of the bone.

In state A (SMNS 4378: Fig. 2.5A, SMNS 5726: Fig. 2.43A), the anterior process of the septomaxilla in front of the external nasal opening is at least 1.5 times the length of the naris. The anterior process is a slender and tapering splint of bone. The same character state is consistently expressed in *Nicrosaurus* species B (Figs. 2.47, 2.55, 2.63).

In state B (SMNS 4379: Fig. 2.8, SMNS 5725: Figs. 2.15, 2.43B), the same part of the septomaxilla is characterised by a figure of less than one naris length. The anterior process is stout and broad, exceeding the width of the naris. The septomaxilla terminates in several distinct prongs which deeply interdigitate with the premaxilla.

(13) nasal borders or is excluded from the antorbital fenestra

BMNH 42743 is the only specimen of *Nicrosaurus kapffi* in which the nasal covers the dorsal process of the lacrimal and enters the antorbital fenestra (Fig. 2.24). The naso-lacrimal suture is still detectable on the internal side of the antorbital rim. In the other specimens, the nasal is well separated from the antorbital fenestra and the bone contacts the lacrimal along the infranasal recess in a complex, serrated suture (Figs. 2.5C, 2.10,

2.12). Since the condition of BMNH 42743 is also representative of *Nicrosaurus* species B, this character is the only variable sutural character that can be correlated with a particular morphological pattern. The external course of the naso-lacrimal suture seems to be linked with the absence of a maxillary flange, and thus is perhaps a result of the increasing verticalisation of the antorbital fenestra.

(14) position of the anterior narial rim relative to the anterior border of the antorbital fenestra

Nicrosaurus kapffi shows considerable variation in the position of the anteriormost point of the external nasal opening. The spectrum ranges from a position slightly in front of the anterior corner of the antorbital fenestra (SMNS 4378: Fig. 2.5A), to level with it (SMNS 5725: Fig. 2.12; SMNS 5727: Fig. 2.18), but also somewhat behind (BMNH 42743: Fig. 2.22) and finally well behind the reference point (SMNS 4379: Fig. 2.8; SMNS 5726: Fig. 2.15).

The dorsal aspect of the skull roof

(15) jugal borders or is excluded from the antorbital fenestra

SMNS 5725 and BMNH 42743 are the only specimens in which the anterior part of the jugal is expanded medially (Figs. 2.12, 2.22). In both specimens, the bone reaches the antorbital fenestra and contributes to the posterolateral border of the opening. The specimens lack the ventral process of the lacrimal, which in the other specimens of *Nicrosaurus kapffi* occupy this position at the posterolateral border of the antorbital fenestra (Fig. 2.43).

(16) jugal borders or is excluded from the orbit (Fig. 2.43)

In external view, the jugal reaches the orbit in SMNS 4379 (Fig. 2.8, right side), SMNS 5726 (Fig. 2.15, left side), SMNS 54706 (Fig. 2.21), and BMNH 42743 (Fig. 2.22). In all these cases, however, the jugal contributes only a small part to the ventral border of the orbit. It is also evident from SMNS 54706, that the jugal only superficially covers the joint between lacrimal and postorbital (Fig. 2.21A), and these bones alone effectively form the internal ventral rim of the orbit (Fig. 2.21B).

(17) concavity of the ventral edge of the jugal

The jugal notch behind the tooth row in the skulls of SMNS 4378 and BMNH 42743 is deeper dorsoventrally (BMNH 42743: 25 mm, compared to 18 mm in SMNS

4379). More conspicuously, the concavity extends more posteriorly, leading to a comparatively slender and more pronounced arch (Figs. 2.5C, 2.24; see comparison Fig. 2.44B and E). This is perhaps a consequence of the less splayed cheeks in both specimens.

(18) orientation of the orbits relative to a horizontal plane

The orientation of the orbits was determined by the inclination of a plane spanned by the orbital rim relative to a horizontal plane, in praxis represented by the skull roof. The orbital plane is set at an angle of 30° to the skull roof in SMNS 4379, which is a good representative of the other robust skulls. This contrasts with the higher value of 40° in BMNH 43743, and 45° in SMNS 4378. Such values, however, have to be treated with some caution, since they are difficult to measure precisely and may be affected by *post-mortem* compaction of the skull. Nevertheless, the difference in orbit orientation among specimens of *Nicrosaurus kapffi* is readily noticeable when comparing the specimens, although a difference of 10 degrees seems to be insignificant in absolute terms. However, it should be borne in mind that in phytosaurs the orbits generally face more dorsally than in other archosaurian groups (SERENO 1993), and thus the total range of observed orientations of the orbital plane is restricted.

(19) dorsal rims of the orbits

While the orbits of SMNS 4379, SMNS 5726, and SMNS 5727 are more or less confluent with the skull, the orbital rims of SMNS 4378 and BMNH 42743 are raised, well rounded, and thinner dorsoventrally (Figs. 2.5C, 2.24). Consequently, the interorbital depression is more deeply developed in these specimens. All these differing characters states can probably be attributed to the more vertical orientation of the orbits, and thus ultimately to the lesser width of the skull. Discrete character states are, however, not clearly recognisable.

(20) orientation (slope) of the cheek

The orientation of the cheek, the plane formed by the jugal, quadratojugal, and the lateral face of the quadrate, is ultimately linked with variation (23) in the relative height of the skull (Fig. 2.44A, D). The higher skulls of *Nicrosaurus kapffi* (SMNS 4378, BMNH 42743) show a somewhat steeper cheek region, which in BMNH 42743 is more obvious and approaches the condition of a vertical lateral skull wall (Fig. 2.22). In the specimens SMNS 4379, SMNS 5726, and SMNS 5727, the angle between skull roof plane and cheek is lower and the cheeks of these three specimens appear to be more splayed (Figs.

2.8, 2.15, 2.18). The increased width of these skulls, however, cannot only be explained by an increased "splayedness" of the quadrates; it represents to some degree also an absolutely broader skull roof (Tab. 2.2.1).

(21) quadratojugal with horizontal depression and flaring ventral rim

The steeper and thinner cheeks of SMNS 4378 and BMNH 42743 are characterised by conspicuous depressions, which lead to a lateral flaring of the ventral parts of the quadratojugals and jugals (Figs. 2.5A, 2.22). In this respect, both specimens match *Nicrosaurus* species B. The depression is not present in the other, more robust specimens, with one exception - the left side of SMNS 4379 (Fig. 2.8). However, the opposite side in this specimen is convex as in SMNS 4279 and SMNS 5727, and the depression is most likely the result of the distortion that evidently affected SMNS 5726, compressing the left side of the cheek.

(22) parietal foramen

The presence of a parietal foramen is evident in SMNS 5726 and SMNS 5727 (Fig. 2.18). It has been argued that occasionally preparational destruction of a covering bony lamina might explain the inconsistent occurrence of the parietal foramen within a taxon (ROMER 1956). This is quite unlikely in *Nicrosaurus kapffi*, given the considerable thickness of the obliterating bone tissue seen in SMNS 54706 (Fig. 2.21B). Both specimens rank above the mean value of skull size of *Nicrosaurus kapffi* (Tab. 2.2.1).

The temporal and occipital region of the skull

(23) width-to-height relation of the skull (Fig. 2.25A, D)

Probably the most striking discrepancies among specimens of *Nicrosaurus kapffi* are the relative height differences of the postorbital part of the skull. In Table 2.2.9, the character is expressed as the ratio of maximal width between the quadrates to maximal skull height measured from the craniomandibular joint to the level of the skull roof (Fig. 2.2). The specimens of *Nicrosaurus kapffi* fall into two well distinguishable categories: a morph with narrow skulls and less widely splayed quadrates (ratio 2.1), both features that lead to the general appearance of a high and tall skull. This morph is represented by SMNS 4378 and BMNH 42743, and is hereafter termed the "high-domed morph". The second morph shows broader skulls (mean value of 2.7, but varying between 2.5 and 2.9). The skull morphology thus appears to be lower than in the first form. This "low-domed morph" includes SMNS 4379, SMNS 5726, and SMNS 5727. The ratios do not

overlap, but suggest genuine dimorphism. Note that the variation in absolute height of the skulls of both morphs is much less than expected from the broad and massive appearance of the low-domed morph, and the values can be regarded as approximately identical (Tab. 2.2.1). The high width of the quadrates correlates with a trend toward a wider skull roof (Tab. 2.2.9) in such specimens. Both the high-domed specimens are more delicately proportioned and have a less robust appearance than the low-domed morphs.

Table 2.2.9 *Nicrosaurus kapffi*, indices of skull measurements.

index	SMNS 4378	SMNS 4379	SMNS 5726	SMNS 5727	BMNH 42743	MEYER (1863: pl. 42 fig. 4)	MCGREGOR (1906: fig. 4)
width quadrate - quadrate / height quadrate - skull roof	2.1	2.7	2.5	2.9	2.1	2.2	2.5
width quadrate - quadrate / width skull roof	2.3	2.3	2.4	2.6	2.3	n/a	n/a
width skull roof / width postorbito-squamosal bar	4.3	3.7/3.4	3.9	3.2	4.0	n/a	n/a
width in % length of postorbito-squamosal bar	indet.	29.7 - 32.5	25.2 - 27	26.4	indet.	nn/a	n/a

Abbrev.: indet. = indeterminable; n/a = not applicable.

The dimorphic character states have already been well illustrated in the two available reconstructions of the skull of *Nicrosaurus kapffi* in occipital view. The outline of the high-domed morph presented by MEYER (1863: pl. 42 fig. 4; here Fig. 2.44A), based on SMNS 4378. MEYER's figure of the occipital aspect differs markedly from MCGREGOR's (1906: fig. 4; Fig. 2.44D, also Fig. 2.41) reconstruction of SMNS 5727 in the much less pronounced relative width. Similarly, GREGORY (1962a: 666) noted an incongruence between the dimensions of MCGREGOR's reconstruction and his own measurements of the specimens, but he erroneously attributed the differences to incorrect reconstructions or poor preservation, rather than variation or dimorphism .

(24) medial rim of the body and the posterior process of the squamosal

The only markedly differing temporal character among specimens of *Nicrosaurus kapffi* can be found in the shape of the medial rim of the squamosal in dorsal view. In SMNS 5727, the postorbito-squamosal bars are parallel to each other (Fig. 2.15). Instead of being parabolically rounded as in the other specimens, the posteromedial rim of the

squamosal (posterior process) on both sides of SMNS 5727 is set at an angle of c. 30° to the anterior medial rim of the bone. The tip of the posterior process of SMNS 5727 is nevertheless rounded and not distinctly pointed (Fig. 2.16, right-hand side of the specimen).

(25) parallel or diverging lateral rims of the skull roof

BMNH 42743 and SMNS 4378 show essentially parallel postorbito-squamosal bars. In SMNS 4379, SMNS 5726, and SMNS 5727, the lateral rims of the postorbito-squamosal bars diverge posteriorly from the midline of the skull. Although the actual degree of deflection is generally not significant (the mean value is 15° divergence from the medial skull axis), it contributes to an absolutely wider skull roof in these specimens.

(26) divergence and slope of the squamosal processes of the parietals

For preservational reasons, features concerning the supratemporal fenestra of a gracile, high-domed specimen can only be determined in SMNS 4378, and are not necessarily representative of the morphotype. The specimen suggests that in the high-domed morph the angle enclosed by the squamosal processes of the parietals is narrower, and the dorsal rims of the processes slope much more gently than in the low-domed morph (compare Fig. 2.44A with 2.44D). However, there is some degree of uncertainty, since the processes have been partially restored recently in SMNS 4378.

(27) length and appearance of the paroccipital process of the opisthotic (Fig. 2.24A, D)

Because the lateral extension of the opisthotic is braced against the medial side of the quadrate and the squamosal, the wider skulls of SMNS 4379, SMNS 5726 and SMNS 5727 (Fig. 2.41) result in a relative elongation of the paroccipital process compared to the high-domed morph. These specimens show also a more massive and wider paroccipital process (Fig. 2.44D), which applies especially to the expanded lateral half of the process (see next topic). The shorter and thus stouter appearance of the paroccipital process is exemplified by SMNS 4378 (Fig. 2.44A).

(28) shape of the expanded lateral part of the paroccipital process of the opisthotic

In *Nicrosaurus kapffi*, the lateral part of the paroccipital process is enlarged ventrally by means of the opisthotic ridge. There are two discrete morphologies within the species:

In SMNS 4378 and SMNS 5727, the ventral opisthotic ridge is confluent with the paroccipital process, merging gradually with the ventral side of the process over some

distance. In the reconstruction Figure 2.41, the morphology of SMNS 5727 was adopted. Nevertheless, there is a ventral expansion of the paroccipital process, but not as demarcated in occipital view as in the second state. In the second morph (SMNS 4379, SMNS 5726), the ventral ridge forms a distinct angle with the ventral side of the basal paroccipital process, which results in a more conspicuous enlargement by a vertical step. The confluent, as opposed to step-like ventral opisthotic ridge, and the effects on the overall shape of the paroccipital process are illustrated in Figure 2.44D and A

(29) supraoccipital borders or is excluded from the foramen magnum

In SMNS 4378 (Fig. 2.26) and SMNS 4379 (Fig. 2.41), the supraoccipital crosses the edge of the supraoccipital shelf and extends downward to form the roof of the foramen magnum. This is in accordance with the configuration in all other phytosaur taxa in which the supraoccipital has been described or figured. By contrast, the exoccipitals clearly meet above the foramen magnum in SMNS 5726 and effectively exclude the supraoccipital from the opening, which is confined to the supraoccipital shelf, at least in external view. Hence the supraoccipital does not consistently contribute to the border of the foramen magnum in *Nicrosaurus kapffi*, in contrast to the impression gained from previous reconstructions (MEYER 1863: pl. 42 fig. 4; MCGREGOR 1906: fig. 4), although these figures correctly show the anatomical condition of the specimen they are based on.

The ventral aspect of the skull

(30) interpremaxillary fossa extraordinarily deep

The depth of the interpremaxillary fossa is substantially enlarged in SMNS 5725 (Fig. 2.13) and SMNS 13078, reaching about one and a half of the value when compared to other specimens.

(31) height of the alveolar ridges

The alveolar ridges are roughly similar in width in all specimens of *Nicrosaurus kapffi*, but in SMNS 4060 (Fig. 2.3A), SMNS 4378 (Fig. 2.5C), and BMNH 42743 (Fig. 2.24), the ridges are much more prominent, deeper and almost fully visible in lateral view below the alveolar rim. This character state is correlated with the alveolar positions of the anterior part of the premaxilla that are set higher and also partially visible from the side.

(32) course of the premaxilla-maxilla suture across the alveolar ridge

In ventral view, the lateral part of the premaxilla-maxilla suture is developed in an acute angular shape showing a long anteriorly pointing prong in SMNS 4379, but simple rounded and transversely oriented in SMNS 4378 (Fig. 2.5B) and SMNS 5726 (Fig. 2.16).

(33) medial shift of maxilla tooth row

In both maxillae of SMNS 5725, the entire maxillary tooth rows are shifted medially relative to the alveolar rim of the bones. The margins of the upper jaws therefore overhang the teeth to a considerable degree (Fig. 2.13). The raised lateral rims of the alveoli still persist and outline the position of the tooth row in an earlier ontogenetic stage. The space between the former lateral rim of an alveolus and the present tooth position is filled by secondary bone tissue, which has, in contrast to the surrounding non-alveolar surface of the maxilla, a smooth appearance dotted with occasional shallow pits.

These modifications are probably a consequence of the extensive lateral expansion of the maxillae in this specimen (topic 33), in combination with the functional need to maintain the maxilla tooth row in close opposition to the posterior dentary teeth. According to the distance of the alveolar rim to the present tooth row, the latter is shifted medially by approximately 20 mm. This suggests a total increase in width of the posterior snout by approximately 15% compared to the snout width at the earlier ontogenetic stage represented by the persisting alveolar rims. Shifting of teeth did not occur in the premaxillae, which is in accordance with the much less lateral flaring of the premaxillae in the anterior part of the snout.

(34) position of the choanae

As far as can be determined, the anterior border of the choanae in most specimens of *Nicrosaurus kapffi* lies exactly below the anterior border of the nares, and there seems to be little variation in this positional relationship. In SMNS 5726, however, the anterior margin of the choanae appears to be shifted forward, although the distance to the anterior narial rim is hardly more than 10 mm. This, however, could well be the result of *post-mortem* distortion.

(35) depth of the palatal vault

The depth of the palatal vault, measured as vertical distance from the posterior end of choana to the level of palatine ridge, is strikingly variable in *Nicrosaurus kapffi* (Tab. 2.2.1). It follows, that in those specimens in which the choanae are placed in a more

dorsal position, the volume enclosed by the postulated secondary palate must have been considerably larger. The functional implications of the deeper choanal and palatal region are unclear, but might be seen as an increase in volume of the nasal cavity, or the air passage. An interpretation is impossible, since the detailed morphology of the nasal cavity and surrounding areas in *Nicrosaurus kapffi* are presently unknown.

(36) reduction of the suborbital opening

The left suborbital fenestra in SMNS 5725 is significantly reduced (Fig. 2.13). A prong of the palatine bridges the middle part of the fenestra and contacts the ectopterygoid. This results in the development of two elongated foramina, which correspond exactly to the somewhat transversely expanded anterior and posterior ends of the suborbital slit seen in the right-hand side. Midway along the palatine-ectopterygoid suture between both foramina there is a round depression filled with matrix, which perhaps indicates the presence of a third foramen. The right suborbital fenestra generally shows the common slit-like shape as in the other skulls of *Nicrosaurus kapffi*. However, there is a marked constriction in the middle part of the opening which may indicate that this fenestra was also in the process of closing at the time of death of the animal. Perhaps GREGORY (1962a: 664) refers to SMNS 5725 when he states that "*Phytosaurus*" *kapffi* has "two small foramina along the posterior palatine suture". This condition is nevertheless atypical for *Nicrosaurus kapffi*.

(37) width of the ventral rim of the jugal and quadratojugal

A character that distinguishes between gracile and robust specimens of *Nicrosaurus kapffi* and is developed in discrete states, is the thickness of the jugal-quadratojugal bar in ventral view, in the posterior part of the subtemporal fenestra. The bar is approximately half as thick in SMNS 4378 (Fig. 2.5B) and BMNH 42743 (Fig. 2.23) and developed as a sharp ridge, compared to the broadly rounded, thick rim of the other specimens in which the lower temporal bar has been preserved (e.g. Figs. 2.16, 2.19).

(38) fontanelle of the basisphenoid

In ventral view, the basisphenoid of SMNS 4379 (Fig. 2.9) is separated in two halves along the midline by a minutely serrated fissure (fontanelle). The larger specimen SMNS 5726 shows the same fontanelle, but only in the anterior half of the basisphenoid (Fig. 2.16). The basisphenoid is undivided without any trace of a fontanelle in BMNH 42743, which is the smallest skull examined (Figs. 2.23, 2.25).

In the following sections, an attempt is made to identify the sources of the observed variation of characters, and list the characters according to ontogenetic (allometric), individual, and sexually dimorphic variation. The discussion, above, of each character that has been identified as variable, focuses on the previous use of these characters at various taxonomic levels. A summary is given in Table 2.2.10. Regardless of the assessment of a character here, the analysis of its variation suggests that these characters are of doubtful value in taxonomy and phylogenetic interpretations of phytosaur relationships. As long as it is impossible to demonstrate that a particular character state does not vary within a clearly demarcated phytosaur taxon, it should be treated cautiously or abandoned altogether.

Table 2.2.10: Intraspecifically variable character states in *Nicrosaurus kapffi* and references documenting the use of the same character in the taxonomy of phytosaurs.

no.	character description	previous taxonomic use
3	shape of the prenarial crest	species level: Long & Murry (1995)
4	width of the crest top	species level: BALLEW (1989)
8	width of the snout	genus level: GREGORY (1962a)
12	length and shape of the septomaxilla	species level: MURRY (1989)
13	nasal borders or is excluded from the antorbital fenestra	species level: CAMP (1936)
14	position of the anterior narial rim relative to the anterior border of the antorbital fenestra	genus level: GREGORY (1962a)
16	jugal borders or is excluded from the orbit	species and genus level: HUNT & LUCAS (1989); HUNT & LUCAS (1991); LONG & MURRY (1995)
18	orientation of the orbits relative to a horizontal plane	species to subfamily level: BALLEW (1989); CAMP (1930); CASE (1922); CHATTERJEE (1978); GREGORY (1962a); HUNT & LUCAS (1991); LONG & MURRY (1995);
20	orientation (slope) of the cheek	species and genus level: BALLEW (1989); LONG & MURRY (1995)
22	parietal foramen	species and subgenus level: CHATTERJEE (1978); HUNT & LUCAS (1991)
23	width-to-height relation of the skull	species to genus level: BALLEW (1989); CHATTERJEE (1978); GREGORY (1962a); LONG & MURRY (1995)
26	divergence and slope of the squamosal processes of the parietals	supra-generic level: BALLEW (1989)
28	shape of the expanded lateral part of the paroccipital process of the opisthotic	species level: BALLEW (1989)
31	height of the alveolar ridges	species level: CASE & WHITE (1934)
34	position of the choanae	subfamily level: LONG & MURRY (1995)
36	reduction of the suborbital opening	supra-generic level: GREGORY (1962a)

2.2.7.2 Ontogenetic variation

Because of the lack of a reasonably continuous growth series in any given phytosaur species, few facts are known about the variability caused by ontogenetic changes of skull characters and allometric growth in the group. In particular, the most important early ontogenetic stages, i. e. embryonic, neonate, and young immature specimens, are virtually absent from the fossil record. There are some juvenile skulls known, but an additional problem is presented by the taxonomic assignment of almost all of these skulls. The skull described by DUTUIT (1977b) as *Paleorhinus magnoculus* is, according to its small size (275 mm) and large orbits, an immature specimen. It seems premature therefore to erect a species or even a separate genus (*Arganarhinus*, LONG & MURRY 1995) based entirely on character states that have elsewhere been suggested to represent juvenility. In my view, *Arganarhinus magnoculus* can be assigned with reasonable certainty as an indeterminate species of a "non-phytosaurid phytosaur" only. CAMP's (1930) "small skulls" of *Machaeroprosopus adamanensis* and *Machaeroprosopus lithodendrorum* probably belong to *Leptosuchus* (LONG & MURRY 1995), but the difficulty of assigning immature skulls is highlighted by the suggestion that at least one of these specimens may represent an adult *Rutiodon carolinensis* (HUNT 1993a: G44). In addition, there are a number of more fragmentary juvenile skulls known from a wide stratigraphic range that presently cannot be assigned to a particular taxon (LUCAS *et al.* 1987).

Previous studies concluded that significant character changes actually take place during growth of the skull (CAMP 1930; COLBERT 1947; LANGSTON 1949; GREGORY 1962a; LUCAS *et al.* 1993; HUNT *et al.* 1997). The differing features of younger skulls for which there is evidence of ontogenetic variation include: a relatively greater snout length; absence of, or less pronounced, ventral and lateral expansion of the posterior parts of the premaxillae; nasal openings not elevated; and a significantly anterior placement of the external nasal openings. LANGSTON (1949) and MURRY (1989) suggested the relatively smaller septomaxilla represented a juvenile character state, and CAMP (1930) listed the smaller size of the antorbital fenestra. However, because of the poor record it is difficult to substantiate any of these claims. The effects of growth on the overall robustness of the skull is impossible to separate from other factors (and *vice versa*), and I agree with BALLEW (1989) that there is not sufficient evidence to support an interpretation of the length of a prenarial crest as a growth-influenced character, as concluded by COLBERT (1947).

Table 2.2.1 shows that *Nicrosaurus kapffi* cannot contribute to a discussion of juvenile character states in phytosaurs. The largest specimens with an estimated skull length of about 900 mm or more, SMNS 5725 and the snout fragment SMNS 13078, however, show several features which are not, or only to a much lesser degree, expressed in the smaller skulls. At present, no size-independent criteria are known to estimate the relative age of individuals in phytosaurs. Provided the assumption that size is a valid indication of the age class of an individual, such specimens may give insight into character states expressed at the far end of the ontogenetic spectrum, i.e. at a stage of old age. This does not automatically preclude such character states from being diagnostic. The state of a character may be taken from "standard"-sized individuals, but it must be kept in mind that such a design might not hold true in smaller or larger individuals, and that there is a risk in applying such characters to taxa of which only a single or a few specimens are known.

Based on this criterion, the characters that can be attributed to ontogenetic variation in Nicrosaurus kapffi are:

variation (2): fusion of the anterior interpremaxillary suture

variation (5): half-cylindrical crest diameter

variation (9): intensive superficial bone remodelling of the prenarial crest

(It is not fully clear, however, whether the pitting is a normal feature that could be associated with somewhat irregular bone growth and old age, or whether it represents an abnormal (pathologic) condition of these individuals. It can be argued that it is more appropriate to attribute the extensive pitting to individual variation, since the crest of the large snout fragment SMNS 13078 shows an essentially unsculptured surface.

variation (11): increased flaring of the maxilla

variation (30): interpremaxillary fossa extraordinarily deep

variation (33): medial shift of the maxillary tooth row

variation (36): reduction of the suborbital opening

The reduction of the suborbital opening as an ontogenetic trait has already been suggested by LANGSTON (1949), but his argument was not based on a growth series, but

on comparison of adult specimens of various species of *Paleorhinus*. The ontogenetic interpretation of the partial closure in *Nicrosaurus kapffi* is somewhat hampered by the observation that the anterior part of the right suborbital fenestra in BMNH 42743, the smallest specimen, seems to be in the process of being separated by two outgrowths of the palatine towards the ectopterygoid.

The suborbital opening in phytosaurs has only once been interpreted in a phylogenetic context. GREGORY (1962a: diagnostic character 11) included the size of the foramen in his generic diagnoses, and he suggested a size reduction in "*Phytosaurus*" and "*Rutiodon*", a group corresponding to the modern Rutiodontinae (LONG & MURRY 1995). However, the character states in GREGORY (1962a) concerning *Nicrosaurus* (his "*Phytosaurus*"), *Mystriosuchus* (at least for *Mystriosuchus* species B, the situation in *Mystriosuchus planirostris* being not fully resolved), and probably *Leptosuchus* and *Pseudopalatus* (both synonymised with *Rutiodon* in that study) as well, are incorrect. A more detailed survey of the number, and shape of the bones surrounding the suborbital fenestra(e) is undertaken in chapter 5 (Appendix B, Tab. B6). The suborbital openings of SMNS 5725 are an important piece of evidence, since they mediate between the character states of one fenestra, as in the majority of taxa, versus two or more that have been reported in two species only. The reduced left side of SMNS 5725 is similar to *Mystriosuchus* species B, in which an anterior palatine-maxilla foramen, a posterior fenestra on the suture of palatine and ectopterygoid, and a tiny foramen between these two are present (HUENE 1911). *Pseudopalatus pristinus* shows an essentially similar condition (MEHL 1928b). Therefore, SMNS 5725 approaches ontogenetically the more derived state of two (or three) discrete suborbital openings. The specimen may, firstly, serve as a model to demonstrate that multiple openings on the palate evolved by subdivision of a single slit-like suborbital fenestra. Secondly, it indicates that all these openings together are true homologues of the single suborbital fenestra. It is very likely that the ontogenetically modified state was established earlier in life in one (or more) clades by heterochrony.

2.2.7.3 Individual variation

The individual nature of varying character states is obvious in the rare case when bilaterally expressed characters are developed differently on each side of the skull (variation 15). Other variations were identified as individual when the distribution is random regarding skull length, or is not obviously correlated with the robustness of specimens and differing height of the postorbital section of the skull.

variation (12): length and shape of the septomaxilla

The character is dimorphic in *Nicrosaurus kapffi*, but the pattern of distribution is neither related to skull-size nor congruent with the character states interpreted here as sex-related dimorphism, and is therefore regarded as individual variation.

The different width of the septomaxilla is very distinctive in individual skulls, but probably an insignificant character in a phylogenetic context. This is not only obvious from the random distribution of the character state in *Nicrosaurus kapffi*, but wide and narrow septomaxillae can even occur simultaneously in one single specimen, as seen in an example of *Mystriosuchus* species B, although in this individual it probably reflects a pathologic condition (HUENE 1911).

MURRY (1989) listed the same two character states of the septomaxilla as a possible feature to distinguish between *Brachysuchus megalodon* (showing the long, tapering state A) and *Angistorhinus alticephalus* (with the short, multipronged state B). However, he then supposed ontogenetic variability of the septomaxilla linked to the robustness of the rostrum, which in his opinion disqualifies its validity as a taxonomically valuable character. The unsuitability of this character for taxonomic purposes is confirmed here, but not for the growth-related reason suggested by MURRY. In *Nicrosaurus kapffi*, the length of the septomaxilla is neither correlated with the rostral morphology (gracility or robustness) nor with the size of the skulls, and therefore the distribution suggests individual variation.

In all specimens of *Nicrosaurus kapffi*, however, there is a notable positive correlation between the length of the septomaxilla in front of the naris with the anterior extent of the nasal. In specimens showing the relatively long septomaxilla (state A above) the nasal is also elongated anteriorly. Those skulls characterised by broad and short septomaxillae (state B) show a correspondingly relatively shorter nasal as well. Individual variation in *Nicrosaurus kapffi* does not affect the observation that in all specimens the septomaxilla reaches far beyond the anterior tip of the nasal. This is the case, regardless of the absolute length of the anterior process of the nasal and the septomaxilla.

variation (13): nasal borders or is excluded from the antorbital fenestra

CAMP (1930) included this character state pair among the diagnostic characters of his various species of *Machaeroprosopus*: the nasal is large, entering the antorbital fenestra in *Machaeroprosopus zunii* and touches the fenestra in both *Machaeroprosopus adamanensis* and *Machaeroprosopus lithodendrorum*. By contrast, it is smaller and separated from the fenestra in *Machaeroprosopus gregorii* and *Machaeroprosopus tenuis*. Since the first three species have been referred to, or synonymised with both species of

Leptosuchus (LONG & MURRY 1995), the nasal reaching the antorbital fenestra could be interpreted as a diagnostic character at the genus level. This is unlikely, however, regarding its variable nature in *Nicrosaurus kapffi*.

variation (14): position of the anterior narial rim relative to the anterior border of the antorbital fenestra

It has long been recognised, that in all phytosaurs except the non-phytosaurid phytosaurs the nares are situated far back on the snout above the anterior half of the antorbital fenestra (GREGORY 1962b; WESTPHAL 1976; BALLEW 1989). This character state represents a synapomorphy of Phytosauridae (BALLEW 1989; chapter 5). A closer survey shows, that in contrast to the precise and uniform formulation of this character in BALLEW (1989: character 9), there are further differences within Phytosauridae regarding the exact location of the nares. These are expressed in the position of the anterior narial tip relative to the anterior corner of the antorbital fenestra: in front of, level with, or behind the latter opening. So, for example, in *Angistorhinus* and *Brachysuchus*, the anterior rim of the naris is located at a point well in front of the level of the antorbital fenestra, but never considerably far behind (MEHL 1913; CASE, 1929; EATON 1965; DUTUIT 1977a). In the more derived *Smilosuchus gregorii*, the narial tip is situated superior to the anterior third or the mid-point of the antorbital fenestra. This could be interpreted as a progressive trend to shift the nares further and further back in more derived phytosaurs, and suggests that the clade Phytosauria might be further resolved using the distance the nares have been moved toward the orbits for defining less inclusive ingroups.

GREGORY (1962b: 656) has already concluded that the position of the naris is unsuitable as a phylogenetic character, at least within advanced phytosaurs (Phytosauridae). This did not hinder him from characterising genera by minor differences in the narial position, nor from distinguishing *Rutiodon carolinensis* from the species he referred to "*Phytosaurus*" by exactly these character states, although he did not put much stress on this point. He then argued, probably correctly, that the variation seen in the position of the nares relative to the antorbital fenestrae, within well defined taxa, does not reflect individual variation with respect to the shifting back of the nasal opening, but actually depends largely on the length of the antorbital fenestra (GREGORY 1962a, b). Regarding GREGORY's interpretation of the phylogenetic value of that feature, there have been considerable changes of opinion about the composition of his operational taxonomic units. Additionally, the rejection was probably based more on the observation that the backward displacement is obviously not linear and thus not congruent with the idea of a progressive advancement of a character and the resulting phylogenetic models.

Mystriosuchus, always considered a highly derived, terminal form, shows the anterior tip of the naris not in a posteriormost position as might be expected, but consistently only at a level with the anterior tip of the antorbital opening. However, non-linearity in character development does not necessarily reduce its phylogenetic and taxonomic value, as long as the character is clearly defined and consistently expressed within operational taxonomic units. The latter is not the case in the species *Nicrosaurus kapffi*. The range of variation in *Nicrosaurus kapffi* encompasses the differences seen in the position of the naris in specimens of *Leptosuchus*, *Smilosuchus*, *Rutiodon*, and *Pseudopalatus*.

variation (16): jugal borders or is excluded from the orbit (Fig. 2.43)

In all non-phytosaurian crurotarsans, ornithodirans, and basal archosaurs, the jugal invariably makes contact with the orbital rim, forming either the whole ventral border or at least part of the ventral rim over a comparatively large distance (CHARIG & SUES 1976; EWER 1965; KREBS 1976; WALKER 1961, 1964, 1990). Thus, the loss of the jugal-orbit contact is most probably the derived character state.

In a broader context, there seems to be a phylogenetic trend among phytosaurs matching the polarity regarding this character. The more primitive forms (non-phytosaurid phytosaurs, *Angistorhinus*) are invariably characterised by the plesiomorphic state, and already CASE & WHITE (1934) noted that the exclusion of the jugal from the orbit only occurs in more derived taxa. The variability at the species level in *Nicrosaurus kapffi*, however, is also seen in *Arribasuchus* (MEHL 1922; CAMP 1930: fig. 11D). This may provide an explanation why the character distribution is apparently disparate within the more advanced terminal taxa (genera): for instance, *Mystriosuchus planirostris* (plesiomorph, MCGREGOR 1906) versus *Mystriosuchus* species B (apomorph, section 3.3) or *Leptosuchus crosbiensis* (plesiomorph: CASE 1922; CASE & WHITE 1934 [*Leptosuchus studeri*]) versus *Leptosuchus adamanensis* (apomorph: CASE 1922). I suspect that in these species the character is individually variable as well, but the situation may be masked by the small sample size and thus a preservational bias. In any case, the distribution of the character states within species and higher categories casts doubts on its taxonomic and phylogenetic validity.

variation (16): jugal borders or is excluded from the antorbital fenestra

In the majority of phytosaurs, the jugal takes part in bordering the antorbital fenestra. A comparison with members of the outgroups (Crurotarsi, Ornithodira) suggests that this condition most likely represents the plesiomorphic character state. The jugal being excluded from the antorbital fenestra is one of the features that was initially used to distinguish between *Mystriosuchus* species B and *Mystriosuchus planirostris*

(HUNT & LUCAS 1989b), the former showing the derived condition. The same character state has even been proposed tentatively to represent a generic difference between *Paleorhinus* and *Arganarhinus* (LONG & MURRY 1995; character difference at species level in HUNT & LUCAS 1991), since the anterior tip of the jugal lies far behind the antorbital fenestra in *Paleorhinus magnoculus*. *Nicrosaurus kapffi* suggests that variability of the character is likely to be found in other phytosaur species as well, and that this character should be avoided in diagnosing species and genera.

variation (22): parietal foramen

CAMP (1930) argued plausibly that in *Leptosuchus* (his *Machaeroprosopus*) the pineal foramen is obliterated during growth, since he observed a persistent parietal foramen only in immature specimens. Similarly, a pineal foramen was found only in the smallest skull of *Mystriosuchus planirostris* (SMNS 13240; subsection 3.2.2). The same developmental trait can be seen in numerous diapsids. Pineal foramina can also occur, rarely, in individual adult specimens within groups that generally lack the opening (e.g. in turtles: GAFFNEY 1975). I do not think, however, that the presence of a parietal foramen in two out of six specimens in which the skull roof is preserved can be called rare. I accept CAMP's suggestion of ontogenetic obliteration, but in addition it is concluded that the superficial closure of the epiphyseal canal progresses at a different pace among individuals in the ontogeny of *Nicrosaurus kapffi*, and the foramen thus may persist even in fairly large individuals.

CHATTERJEE (1978) included a persistent parietal foramen in his diagnosis of *Paleorhinus*, although only one specimen referred to by him to that genus, the type of *Paleorhinus scurriensis*, actually shows the character state (LANGSTON 1949). Without mentioning *Paleorhinus scurriensis*, GREGORY (1962a) and HUNT & LUCAS (1991) distinguished *Mesorhinosuchus fraasi* from all other adult phytosaurs by the presence of the same character, based on JAEKEL's (1910) description. The validity of a persistence or absence of the parietal foramen has already been questioned by MURRY (1989) based on CAMP's ontogenetic reasoning outlined above. The individual variation seen in *Nicrosaurus kapffi* suggests that the same may hold true for *Paleorhinus* and *Mesorhinosuchus*, and further substantiates the opinion that this is an unsuitable taxonomic character.

variation (24): medial rim of the body and the posterior process of the squamosal

The angular posteromedial rim of the squamosal in SMNS 5727 is strikingly similar to that of *Nicrosaurus* species B SMNS 12593 (Fig. 2.49) and *Nicrosaurus* sp. BMNH 38037. The significance of the congruence is discussed in part 2.4.3.1.

In general, many aspects of the temporal region of *Nicrosaurus kapffi* such as the size of the supratemporal fenestra, the length and width of the postorbito-squamosal bar, the shape of the parieto-squamosal bar, and characters of the supraoccipital shelf are remarkably congruent among the specimens. This all underlines the suggestion that temporal characters are useful and important for taxonomy and phylogeny.

variation (28): shape of the expanded lateral part of the paroccipital process of the opisthotic

Comparable confluent shapes of the ventral opisthotic ridges are found consistently within *Angistorhinus*, *Leptosuchus crosbiensis* (BALLEW 1989), *Leptosuchus adamanensis* (CAMP 1930: pl. 2), and *Smilosuchus gregorii* (CAMP 1930: pl. 4; COLBERT 1947: pl. 7 fig. 3).

A well demarcated ventral opisthotic ridge perhaps corresponds to the morphology of the paroccipital process of the opisthotic described by BALLEW (1989) with the term "oar-shaped". The two opposite character states as figured in BALLEW (1989: fig. 2B, D) are similar to the shape differences of the opisthotic in *Nicrosaurus kapffi* (Figure 2.44A, D). BALLEW (1989: character 45) identified the "thin and elongated" opisthotic as an autapomorphy of *Arribasuchus mccauleyi*, in contrast to the plesiomorphic oar-shaped paroccipital process of *Arribasuchus buceros* and *Pseudopalatus pristinus*. However, the variability seen in *Nicrosaurus kapffi* suggests that the shape of the lateral part of the paroccipital process is an unsuitable diagnostic character at the species level. This is supported by *Pseudopalatus pristinus*, which is also strongly variable regarding this character (MEHL 1928b; BALLEW 1989: fig. 2D). All specimens of *Mystriosuchus* show a similar step of the ventral opisthotic ridge, but the ridge is usually less broad than in the other taxa. The distribution of the character states reported so far among phytosaurs suggests that the peculiar step-like mode of enlargement of the paroccipital process was acquired in a clade within Phytosauridae (part 5.4.3.3; node K in BALLEW 1989: fig. 1), but that individual development may be variable.

variation (29): supraoccipital borders or is excluded from the foramen magnum

The informativeness of the character states "supraoccipital participating at foramen magnum" and "supraoccipital excluded by exoccipitals" has been considered doubtful in a study on basal archosaur phylogeny (GOWER & SENNIKOV 1996). This conclusion is further substantiated, not only by the disparate distribution of the character within phytosaurs, one of the ingroups of that study, but also by polymorphism at the species level of one of the ingroup taxa.

variation (32): course of the premaxilla-maxilla suture across the alveolar ridge

DOYLE & SUES (1995; fig. 2) noted the marked "zig-zag" course of the suture between premaxilla and maxilla across the alveolar ridge in specimen SMP VP-45 referred to *Rutiodon carolinensis*, and suggested tentatively that this character state might be autapomorphic for this taxon. The variable condition within *Nicrosaurus kapffi* casts doubt on the validity of this potential autapomorphy.

variation (34): position of the choanae

Regardless of the interpretation of the more anterior position of the choanae relative to the nares in SMNS 5726 as genuine or a *post-mortem* artefact, the importance of the condition seen in all except one specimen of *Nicrosaurus kapffi* lies in the fact that it invalidates a character used by LONG & MURRY (1995) to define Rutiodontidae. In this family, which was erected to include *Angistorhinus*, *Brachysuchus*, *Rutiodon*, *Nicrosaurus*, *Pseudopalatus*, and *Arribasuchus*, the choana is said to be placed posterior to the naris. This is evidently misinterpreted for *Nicrosaurus kapffi* and, according to CASE (1922, 1929) and GREGORY (1962a), the choana is in a similar position to that of *Nicrosaurus* in the remaining genera, except for *Angistorhinus* and *Brachysuchus*.

variation (35): depth of the palatal vault

There seems to be a trend towards deeper palatal vaults in high-domed, gracile specimens (SMNS 4378, BMNH 42743: Tab. 2.2.1), although the robust skull SMNS 5727 (Fig. 2.19) has a palatal depth far exceeding that of the other specimens. The greatly increased depth in SMNS 5727 cannot be explained by *post-mortem* deformation. It should be noted that the same trend is also detectable in the low-domed and high-domed skulls of *Nicrosaurus* species B (Tab. 2.3.1). In this species, the depth of the palatal vault forms an almost perfect continuum decoupled from skull-size rather than being dimorphic. The character is tentatively regarded as individually variable.

variation (38): fontanelle of the basisphenoid

The evidence shows that in *Nicrosaurus kapffi* (and *Nicrosaurus* species B, see subsection 2.3.2) there is individual variation from a basisphenoid corpus in two halves, which are at least superficially divided and probably joined in life by a synchondrosis, to a normal uniform basisphenoid. The functional and developmental significance of this is difficult to explain, especially since the braincase in phytosaurs in general not only tends to be intensively ossified, but also because there is no evidence known which might

suggest that the corpus of the tetrapod basisphenoid fuses from separate ossification centres.

Incompletely united basisphenoids have escaped attention so far in other phytosaurs. In the closely related Aetosauria, PARRISH (1994) mentions the presence of a fontanelle on the ventral side of the basisphenoid in *Longosuchus* and *Desmatosuchus*, and subsequently suggested the character as synapomorphic for these two genera. However, the fontanelle is said to be hemispherical between the tuberal part and the basipterygoid processes, which probably means running transversally across the bone. In this case, the fontanelle could be interpreted as a persisting fenestra basicranialis of the embryonic basal plate. The fenestra basicranialis is a growth zone separating the ossifying basioccipital and basisphenoid that persists in neonate lacertilians (e.g. RIEPPEL 1992a, 1992b). In any event, it is a different structure from the fontanelle seen in *Nicrosaurus*. The variation in both *Nicrosaurus* species precludes a practical apomorphic interpretation of this structure.

2.2.7.4 Sexual variation

HUENE (1909, 1911: 93) was probably the first author who considered the presence of sexual dimorphism in phytosaurs, although only in passing and only regarding a single character. He interpreted the premaxilla crest of *Mystriosuchus* species B as a pathological outgrowth on the snout, and suggested that such crested forms might be males. ABEL (1923, 1935) again brought up the topic and put forward an extreme version of a sex-related prenarial crest variation in phytosaurs. As the main developmental process in forming a prenarial crest he suggested the accumulation of lesions sustained in interspecific combat. In other words, since males were in his experience more frequently involved in territorial and dominance conflicts, the crested specimens are males, the uncrested females. Consequently, he concluded that there are only two monotypic genera of phytosaurs: the European form *Phytosaurus* (*Nicrosaurus kapffi* being the male, *Nicrosaurus* species B and *Mystriosuchus planirostris* the female morph), and its North American counterpart *Rutiodon*, including "male" *Arribasuchus* and "female" *Rutiodon carolinensis*.

ABEL's interpretation was challenged immediately on the grounds of insufficient and weakly founded developmental evidence (MOODIE 1923) and consistency in the spatial and temporal distribution of the specimens involved (WESTPHAL 1976), and the idea never gained wide acceptance. Nevertheless, the idea of sexual dimorphism in phytosaurs was evidently stimulating and, since ABEL's times, phytosaurs never lost the attribute of highly sexually dimorphic archosaurs. When the number of North American

phytosaur specimens increased constantly in the following decades, sexual dimorphism proved highly intriguing as an explanation of observed conflicting character distributions. A number of studies focused on this topic, and various features have been considered likely to be correlated, fully or in part, with sex and were subsequently utilised to distinguish between the genders in phytosaur taxa. Briefly summarised, the following characters have been suggested as predominantly sex-related:

(1) degree of robustness of the skull: broad and heavy in males, more delicate in females (CAMP 1930; COLBERT 1947; WESTPHAL 1976).

(2) elevation of the external nares to a crater-like appearance relative to the pre- and postnarial area: in females crater-like, in males absent or less developed (CAMP 1930; COLBERT 1947; GREGORY 1962b; WESTPHAL 1976).

(3) presence and/or extent of a prenarial crest: present in all males and adult females, lacking in immature females (COLBERT 1947; GREGORY 1962b; WESTPHAL 1976; MURRY & LONG 1989, but later abandoned in LONG & MURRY 1995).

BALLEW (1989) rejected all previous suggestions of sexually dimorphic characters on the grounds that they are not testable at present, both because of preservational reasons (incompleteness, distortion) and the lack of a representative sample size of clearly contemporaneous and sympatric specimens. Consequently, she regarded all characters listed above as taxonomically useful. There is no doubt that both arguments apply to all phytosaur species. Because of the lack of a sufficiently large sample, supposed variability (whether sexual or ontogenetic) of a particular skull character can presently neither be substantiated nor disproved by statistical means in any phytosaur taxon.

I agree that a number of characters suggested as sexually variable in phytosaurs (e.g. narial elevation, prenarial crest length) are unsubstantiated at present. However, I think that BALLEW's conclusions are too strict and unbalanced. An assumed or obvious preservational bias can be largely avoided by either excluding strongly affected specimens from the study or by reconstructing, or at least estimating, the original shape of a specimen. Whereas there might be problems with characters showing a relatively narrow range of differences (e.g. the degree of naris elevation or the height of prenarial crest), regarding numerous characters suggested as dimorphic in *Nicrosaurus kapffi* below (e.g. differing relative skull width, most prenarial crest characters), even strongly distorted specimens can still be accurately categorised. Furthermore, a brief survey of the literature shows that only a few hypotheses of sexual dimorphism or sex-related character

variability in fossil vertebrates (including hominids), that have been put forward and are widely accepted, can be supported by statistical tests.

Requirements and criteria for determining sexual dimorphism

Statistics is perhaps the most powerful, but not the only means to test a hypothesis on sexually induced variation. There are a number of requirements and criteria that are essential to interpret character state differences as sexual variability, or that should be fulfilled in ideal cases. Does *Nicrosaurus kapffi* match such requirements?

Requirement (a): Monophyletic taxon which is likely to represent a biological species

The taxonomic status and the composition of the North American forms (*Leptosuchus*, *Smilosuchus*, *Pseudopalatus*, *Arribasuchus*), on which the more recent studies of sexual variation are based, has been frequently questioned and revised. The taxonomic debate is still far from being settled (e.g. BALLEW 1989; HUNT 1993a, 1993b, 1994; LONG & MURRY 1995). The only taxon that has received general approval is *Smilosuchus gregorii*. By contrast to this situation, *Nicrosaurus kapffi* is defined by several clearly autapomorphic characters, which strongly support the monophyletic status of the taxon. Since MEYER's (1863) description there was an almost unchallenged consensus that *Nicrosaurus kapffi* represents a valid species. If there is a phytosaur taxon suitable for studies of variation of any kind, then it is *Nicrosaurus kapffi*.

Requirement (b): Sympatric and contemporaneous specimens

There is no question about the sympatric occurrence of *Nicrosaurus kapffi*; to our knowledge, the species is geographically restricted to the area around Stuttgart in central Württemberg. The stratigraphic match of the specimens is less determined (see Appendix C). At least the earlier found specimens (including examples of different morphs, the high-domed SMNS 4060 and SMNS 4378, and the low-domed SMNS 4379) are likely to be derived from the same locality. The whole sample comes from a very limited stratigraphic range, the lower and middle Stubensandstein at most, spanning, in total, approximately 70 metres of fluvial deposits (BRENNER 1973, 1978a). The stratigraphy of the North American Chinle Formation and Dockum Group is much more complex and stratigraphic units are in constant modification. Note that, with the exception of the Canjilon quarry (BALLEW 1989; HUNT & LUCAS 1989a; LONG *et al.* 1989), almost all phytosaur taxa are spread over several localities, which are difficult to correlate precisely

(LONG & MURRY 1995: 226-230). Correlations of vertebrate sites over larger distances are particular difficult, and consequently different schemes are in existence (LONG & MURRY 1995).

Requirement (c): Reasonable sample size

The sample under consideration includes three complete skulls (SMNS 4379, SMNS 5726, SMNS 5727), two skulls lacking parts of the temporal region (SMNS 4378, substantial loss in BMNH 42743), one incomplete skull (SMNS 5725), and a further three rostral fragments (SMNS 4060, SMNS 13078, SMNS 54708). While the total of nine specimens is not sufficient to allow the application of statistical tests, and also not ideal compared to other studies of sexual variation in fossil reptiles (e.g. DODSON 1976; RAATH 1990; WEISHAMPEL & CHAPMAN 1990), the sample is quite reasonably sized in relation to the known specimens of well known phytosaur species (e.g. CHATTERJEE 1978; LONG & MURRY 1995: 226-230).

Criterion (a): Pattern of variation

Character states that are obviously subject to ontogenetically induced variation (i.e. that are correlated with size) have been dealt with in the preceding subsection and are not included in the present category. It is more difficult to segregate sexual variation from other sources of variability. RAATH (1990) used a size-frequency pattern in characters with clearly distinguishable dimorph states in the theropod *Syntarsus*. He distinguished sexual from ontogenetic variation in these characters, in which the complementary character states were found to be expressed only in specimens that have passed a certain size threshold. The underlying assumption in RAATH's work is that sexually variable features only develop near maturity, i.e. after reaching a certain size, whereas, for example, individual variation is size-independent and should occur in all age classes. Individuals below this empirically determined threshold invariably showed only one character state, in this case the character states coupled with the gracile morph. However, a more complete ontogenetic series than exists for *Nicrosaurus kapffi* is needed to establish such a threshold and to clearly distinguish between a genuine size-frequency and a randomly induced pattern. DODSON (1976) identified sexually variable characters in *Protoceratops* by principle coordinates analysis. Again, the sample size in *Nicrosaurus kapffi* is too small to attempt a similar approach.

Criterion (b): Character congruence

An obvious criterion is the occurrence of the same character in extant closely related animals, in which it can be proved to be sex-dependent. This is difficult for phytosaurs, because in their nearest living relatives, crocodiles, there are no reports of substantial sexual dimorphism expressed in the skull morphology or osteology. This may be an indication of the non-existence of sexual dimorphism, at least as expressed in the skeleton, but could also represent the poor knowledge of such variation in this group. An important, and at the moment probably the only independent and applicable test method, is the congruence of correlated character state pairs within the sample, especially when both characters are not directly morphogenetically related and there is a strong case that one of them is favourable in intraspecific interactions, such as attraction of mates, repulsion of rivals, or dominance in social or territorial behaviour. For instance, the relative height of the skull and a number of the prenarial crest characters are both dimorphic in *Nicrosaurus kapffi*, and the character state distribution is congruent. The morphology of the prenarial crest probably affects the impact of the structure as a visual sign, and could be interpreted as a secondary sexual character analogous to various display structures among recent reptiles. There is no obvious explanation of how the dimensions of the postorbital skull could influence, for example, the sculpture or the shape of the prenarial crest. On the other hand, the height of the skull directly controls (or is actually the result of) a number of other character states, for example the orientation of the orbits or the slope of the cheek, and these form an integrated system. Such correlations, as conspicuous as they are, do not further support a hypothesis of sexual variation, but rather demonstrate morphogenetic constraints. The interpretation of particular dimorphic character states as possibly sexually variable in *Nicrosaurus kapffi* is in part supported by the presence of similar character state pairs observed within other clearly defined and generally accepted phytosaur taxa.

Characters of the postorbital part of the skull: morphogenetically correlated dimorphic characters

COLBERT (1947: 70) interpreted the presence of robust and gracile morphs among the Chinle phytosaurs as a general indication of sex and arbitrarily referred the robust skulls to males, although he almost certainly had a multispecific assemblage at his disposal (BALLEW 1989; LONG & MURRY 1995). The same distinction is obviously present in *Nicrosaurus kapffi*. However, it is difficult to identify a non-arbitrary and

measurable threshold between robust and gracile forms, and the robusticity of a skull is almost certainly influenced by growth factors. *Nicrosaurus kapffi* shows a limited size range, so that the influence of growth on the specimens available may be largely neglected. The general build of the skull, however, coincides with the much more obvious character state pair (23), and the specimens are grouped according to these characters in Figure 2.1.

variation (23): width-to-height relation of the skull

The intraspecific variation of the width-to height ratio of the postorbital skull in *Nicrosaurus kapffi* is supported by the presence of a high-domed and low-domed morph in at least one other well-known species: *Smilosuchus gregorii*. The referred specimen AMNH 3060 (COLBERT 1947: pl. 7 fig. 3) has a much narrower and significantly higher skull than the holotype of the species (CAMP 1930: pl. 5). In this genus, the skull height differs also in absolute values, and the ratios between both morphs seem to be even more disparate than in *Nicrosaurus kapffi* (Tab. 2.2.9). The same morphotypes are also readily distinguishable in *Nicrosaurus* species B (part 2.3.4.2)

Although both high-domed specimens of *Nicrosaurus kapffi* show a comparatively small skull size, the character state probably does not represent ontogenetic variation. SMNS 4379 (Figs. 2.8, 2.10), the most typical representative of the low-domed morph, is of similar size, and all three specimens are unlikely to be juveniles.

GREGORY (1962a: 666; tab. 2; character no. 7 in the diagnoses of genera) introduced the width-to-height proportion of the skull as a generic determinant in the form of "tall quadrate". He chose the height of the quadrate in relation to skull roof width, because the skull width between the quadrates is said to be frequently affected by distortion. In this study, the effects of distortion were corrected by taking the distance between the quadrate and the skull mid-line at the occipital condyle of the less distorted half and doubling this amount (Tab. 2.2.1). I also find it difficult to determine exactly the height of the quadrate; the distance between the base of the quadrate and the skull roof is easier to measure.

Concerning GREGORY's (1962a: tab. 2) taxonomic results, it is noteworthy that the range of his values (i.e. the standard deviation) is increased significantly as soon as three or more skulls per taxon were included. This is evidently not a result of GREGORY's taxonomic units, but applies especially to generally accepted species like *Nicrosaurus kapffi* and *Mystriosuchus planirostris*. The wide range suggests intraspecific variability, and renders especially the extreme individual values almost useless for the intended taxonomic purpose. Several authors followed GREGORY's suggestion and claimed that

skull width was diagnostic at the genus level (CHATTERJEE 1978; LONG & MURRY 1995; MURRY 1989).

The same differences in skull proportions were also employed as taxonomic criteria at the species level. MURRY (1989: 126) suggested that relative skull height distinguished between *Brachysuchus megalodon* and *Angistorhinus alticephalus*, LONG & MURRY (1995: 46) interpreted the wide postorbital skull of *Smilosuchus gregorii* as autapomorphic ("derived character"), and BALLEW (1989: 321, character 22) introduced the "quadrates pulled in toward the midline of the skull" of *Leptosuchus crosbiensis* as autapomorphic for the species. This character represents an unquantified expression for the width-to-height relationships of the postorbital part of the skull. LONG & MURRY (1995: 43) rejected this distinction on the grounds that it may partially reflect preservation, and distortion may result in "flared quadrates" i.e. wide-skulled specimens.

A number of characters of the postorbital section of the skull are causally linked with the width-to-height ratio of the skull. The differing character states may be either a direct result of the variable skull width, or they may actually control the morphological development of the shape of the postorbital section.

variation (18): orientation of the orbits relative to a horizontal plane

In the low-domed morph of *Nicrosaurus kapffi*, the orbits face more dorsally than in the high-domed specimens (Fig. 2.44B, E). The orientation of the orbits has been assessed as an essential part in almost every generic and specific diagnosis. The practical value of the character, however, is severely restricted for two reasons. Firstly, it is difficult to recognise discernible character states for the orientation of the orbits. In practice, the angle of the plane of the orbit is difficult to measure and always includes a significant error margin. The character definition is probably, for that reason usually not given in absolute and testable values, but in unspecific, relative terms such as orbits "directed dorsolaterally", "facing more outward", or "facing more upward" (e.g. BALLEW 1989; CHATTERJEE 1978; LONG & MURRY 1995; MURRY 1989). These terms perhaps correspond to an angle of about 45°, or more than, or less than this amount. Applying such categories to *Nicrosaurus kapffi* illustrate the subjectivity of the character state distinction. In both morphs the orbits face general dorsolaterally, rather than dorsally or laterally. However, do the orbits in the high-domed morph still face dorsolaterally, or more upward (the latter is certainly the case in respect to the low-domed morph)? It is not possible to refer the high-domed morphs objectively to one of these categories.

Secondly, even using arbitrary and relative distinctions, the character distribution is at variance with established taxonomic and phylogenetic schemes based on more discrete features, and indicates that the different degree of orientation of the orbits is either achieved convergently or is variable at the level of lower categories. In his phylogenetic interpretation, CHATTERJEE (1978) correctly discarded the orientation of the orbit as being variable, attributing the discrepancies to growth differences and crushing, but did not present substantiating evidence for this explanation.

Furthermore, the polarity of the character transformation is unknown. BALLEW (1989: character 6) suggested dorsally facing orbits as synapomorphic for *Paleorhinus*. However, the character state is not present in "*Parasuchus hislopi* " (CHATTERJEE 1978) and *Paleorhinus sawini* (LONG & MURRY 1995), of which only comparatively high-domed specimens are known. CAMP (1930) and LONG & MURRY (1995) used the character for discrimination at the subfamily level, which is even more dubious because subfamilies necessarily include genera which show a varying degree of orbit orientation (e.g. *Paleorhinus*, *Angistorhinus*, *Smilosuchus*, and *Nicrosaurus*).

variation (20): orientation (slope) of the cheek

Both conditions described above were introduced by BALLEW (1989) as autapomorphies of two different species. "*Rutiodon*" [= *Smilosuchus*] *gregorii* was characterised, among others, by the characters "jugal no longer meets quadrate in a lateral plane; quadrate has angled upward and outward" (p. 313: character 28; p. 323). This describes the condition of the low-domed morph of *Nicrosaurus kapffi*. "*Rutiodon*" [= *Leptosuchus*] *crosbiensis* was distinguished from other "*Rutiodon*" by the complementary character state, "quadrates pulled in toward the midline of the skull" (p. 313: character 22; p. 321), which effectively results in a steep cheek comparable to the high-domed morph of *Nicrosaurus kapffi*. There are several severe problems with this character state pair when applied in a phylogenetic analysis.

(a) As in *Nicrosaurus kapffi*, the character is obviously polymorphic in the species *Smilosuchus gregorii*. Specimen AMNH 3060 matches the character description given for *Leptosuchus crosbiensis* (see COLBERT 1947: pl. 7 fig. 3). This invalidates the autapomorphic status of the character state.

(b) The polarity of the character is difficult to establish, since an outgroup comparison with *Paleorhinus* and *Angistorhinus* remains inconclusive. The more derived *Pseudopalatus* and *Mystriosuchus* have consistently almost vertical cheeks, which might suggest that the verticalisation is the derived condition.

(c) BALLEW interpreted both character states as apomorphies within the unresolved clade "*Rutiodon*" (1989: fig. 1, node F). This is only possible, if an intermediate state is

hypothetically assumed to represent the plesiomorphic condition of the last common ancestor of the terminal taxa above node F. Such a condition might be represented by "*Rutiodon*" [= *Leptosuchus*] *adamanensis*, which shows "a more laterally flared skull" (BALLEW 1989: 323) than *Leptosuchus crosbiensis*. The presence of an intermediate character state within the same clade renders character state recognition almost impossible, since it can be expected that individuals also show some variation or preservational distortion.

BALLEW (1989: character 29) listed the more dorsoventral orientation of the infratemporal fenestra as a separate autapomorphy of *Smilosuchus gregorii*, although she noted that this is directly related to the slope of the cheek (BALLEW 1989: character 28). Hence, the discussion of variation (20) applies to this character as well.

variation (25): parallel or diverging lateral rims of the skull roof

variation (27): length and appearance of the paroccipital process of the opisthotic

The same distinction for both morphs of *Nicrosaurus kapffi* is found when comparing both morphs of *Smilosuchus gregorii* (CAMP 1930: pl. 5; COLBERT 1947: pl. 7 fig. 3), or *Arribasuchus mccauleyi* (BALLEW 1989: fig. 2C) with *Arribasuchus buceros* (HUENE 1915a: fig. 11d). It should be noted that *Arribasuchus mccauleyi* is not a generally accepted species (HUNT 1994; LONG & MURRY 1995).

The correlation of the six character states in *Nicrosaurus kapffi* listed above, shows that these features are likely to form an interdependent character complex. It is thus misleading to introduce each character (e.g. orientation of the orbit, slope of the cheek, and orientation of the infratemporal opening) separately in a phylogenetic analysis.

The intraspecific variability of the skull width in *Nicrosaurus kapffi*, regardless of whether its interpretation as sexual variation is accepted or not, and consequently the corollary effects on the listed characters of the postorbital region, cast serious doubts on the taxonomic value of these features in phytosaurs at the specific level. For *Nicrosaurus kapffi*, the variability of the character states argues strictly against their interpretation as diagnostic features, and it is difficult to see how characters with such a range of mostly gradational character states can be incorporated into a meaningful diagnosis of the taxon. This does not automatically imply that the taxonomic use of the same characters must be rejected for other taxa, but each operational taxonomic unit needs to be tested separately for variability. Presently, the only phytosaur taxa for which an invariable character state (i.e. consistently high and narrow skulls) can be demonstrated on the basis of several specimens, are *Mystriosuchus planirostris* and *Pseudopalatus pristinus*. For the time

being, it seems advisable not to found lower-category taxa on one of the listed characters, as long as the sample size does not allow determination of the range of intraspecific variability. This applies especially to species that are based on a single specimen only, such as *Paleorhinus sawini* (LONG & MURRY 1995), *Paleorhinus magnoculus* (DUTUIT 1977b), *Arribasuchus mccauleyi* (BALLEW 1989), and *Mystriosuchus* species B (this paper).

At a more inclusive level, the characters (18), (20), (23), (25), and (27) were suggested to be more informative (GREGORY 1962a; CHATTERJEE 1978). For example, the majority of recognised species of non-phytosaurid phytosaurs show a moderate to low-domed posterior part of the skull ("*Parasuchus hislopi*", *Paleorhinus scurriensis*), among which the lateral skull profile can decrease to an almost flat outline (*Paleorhinus bransoni*, *Paleorhinus ehlersi*, *Ebrachosuchus neukami*, *Paleorhinus magnoculus*). However, LONG & MURRY (1995) recently described the first high-domed skull in *Paleorhinus* as a new species, *Paleorhinus sawini*. The compilations of GREGORY (1962a: tab. 2) and CHATTERJEE (1978: tab. 3) show that it is impossible to recognise discrete character states among most of the genera. This is a logical consequence of the inter- and intraspecific variation.

It would also be of interest to carry out detailed examinations of more well-represented taxa, such as *Leptosuchus*, focusing on the variability of these characters. Among the two presently established species, based on differences in temporal characters (BALLEW 1989; LONG & MURRY 1995), but also skull width (BALLEW 1989), *Leptosuchus crosbiensis* represents a high-domed form (BALLEW 1989: fig. 2A), while the occipital aspect of *Leptosuchus adamanensis* (CAMP 1930: pl. 2) corresponds proportionally to the low-domed morph of *Nicrosaurus kapffi*. Skull morphology in *Leptosuchus* is apparently considerably variable, and the most recent review admits that the segregation into two species is tentative and remains debatable (LONG & MURRY 1995). The presence of the same dimorphic characters in the accepted species *Nicrosaurus kapffi* may even suggest that *Leptosuchus* is a highly variable monospecific assemblage.

Characters of the crest in the prenarial region correlated with the width-to-height ratio of the skull

variation (3): shape of the prenarial crest

The previous taxonomic use of this character by LONG & MURRY (1995) is discussed and rejected in part 2.2.4.3 (ii).

variation (4): width of the crest top

variation (6): steepness of the crest flanks

variation (7): sculpture on the flank of the crest

Characters of the rostrum correlated with the width-to-height ratio of the skull

variation (1): degree of expansion of the snout tip

variation (8): width of the snout

The width of the snout is one of the main characters that led GREGORY (1962a) to subdivide phytosaurs with a depressed border of the supratemporal opening and a long posterior process of the squamosal into those with massive snouts ("*Phytosaurus*"), and with less massive to slender rostra ("*Rutiodon*"). GREGORY's taxonomic distinction is essentually similar to the ecological classification that was already put forward by CASE (1929, 1931, 1932a) and CASE & WHITE (1934) as brachysuchan and leptosuchan phytosaurs, and recently revived under the attributes brachyrostral versus altirostral and dolichorostral types of phytosaur snouts (HUNT 1989). BMNH 42743 demonstrates that specimens of the "massive snouted" *Nicrosaurus kapffi* can have significantly narrow snouts.

variation (10): steepness of the lateral face of the maxilla (presence of a maxillary flange)

variation (31): height of the alveolar ridges

The prominence of the alveolar ridges as expressed by their visibility in lateral view was employed, among other characters, in the differential diagnosis of *Leptosuchus studeri* by CASE & WHITE (1934). The condition in *Nicrosaurus kapffi* suggests that the character is most likely intraspecifically variable in this taxon (and in *Leptosuchus crosbiensis*, LONG & MURRY 1995) as well.

Other skull characters correlated with the width-to-height ratio of the skull

variation (17): concavity of the ventral edge of the jugal more pronounced

variation (19): dorsal rims of the orbits

variation (21): quadratojugal with a horizontal depression and a flaring ventral rim

variation (26): divergence and slope of the squamosal processes of the parietals

The taxonomic and phylogenetic utility of this character is further discussed in part 2.2.4.3 (v). The squamosal processes of SMNS 4378 resemble much more the condition in *Nicrosaurus* species B (section 2.3; Fig. 2.54), but differ from this taxon in being vertical and practically does not overhang the supraoccipital shelf, and therefore lacks an occipitally facing groove. SMNS 4378 also lacks other characteristics of the temporal and occipital regions of *Nicrosaurus* species B, most notably an elongated supraoccipital shelf.

variation (37): ventral rim of the jugal and quadratojugal narrow and sharp

The morphology of the high-domed morph of *Nicrosaurus kapffi* resembles the situation in specimens of *Nicrosaurus* species B (especially the corresponding high-domed morph) in a number of features. Particularly striking among these are the less splayed and narrower cheeks (including the corollated characters 18, 23, 25, and 27), the narrowness of the rostrum (8), and the deep palatal vault (35). There is also a similarity in minor morphological details including all features of the rostrum and characters (17), (19), (21), (25), and (37). The resemblance is strongly enhanced in the more gracile skulls of the high-domed *Nicrosaurus kapffi*, and all *Nicrosaurus* species B. When comparing BMNH 42743 with, for example, a typical low-domed specimen such as SMNS 4379, and disregarding the derived characters of the species, but applying overall similarity as guidance, it is readily understandable that several authors (e.g. Huene 1909, 1911; Abel 1923) came up with the idea that such a specimen might represent a grade between *Nicrosaurus kapffi* and *Nicrosaurus* species B.

Finally, it should be noted that the "super-gracile" specimen BMNH 42743 is also the smallest skull of the sample. This might indicate that gracility is enhanced in younger

individuals in combination with the presence of the correlated character states, and perhaps these characters are typical of smaller-sized *Nicrosaurus kapffi*. Such a pattern would be analogous to the theropod *Syntarsus*, in which robusticity and thus the manifestation of the gracile and robust morphs with the correlated dimorph characters is only acquired after attaining a body size that suggests sexual maturity (RAATH 1990). Following this study, a distinction of robust and gracile forms among archosaur species has often been interpreted as an indication of sexual dimorphism (CARPENTER 1990; WEISHAMPEL & CHAPMAN 1990).

Section 2.3
Nicrosaurus species B
("*Belodon plieningeri*" sensu MEYER 1861)

2.3.1 History of taxonomy and research

Among the material under study, *Nicrosaurus* species B posed the most problems in terms of both taxonomy and nomenclature in the past. This is reflected in the complex and confusing taxonomic history of the specimens referred here to this taxon.

SMNS 4059, the first find of a more substantially preserved phytosaur skull in Europe made near Heslach in 1859, was referred by MEYER (1860a) to *Belodon plieningeri* and allowed him later (MEYER 1861: 346) to redefine and substantiate his concept of this species (WESTPHAL 1963b, GREGORY & WESTPHAL 1969). It was certainly MEYER's intention to clarify the status of the former tooth taxon *Belodon plieningeri*, and one could even argue that the account fulfils the modern requirements for designating a neotype for the species. The incomplete nature of the specimen and its poor preservation, however, prevented MEYER from fully understanding the anatomy of a phytosaur skull. He confused the antorbital fenestrae with the orbits, the orbits with the supratemporal openings, and consequently misidentified a number of skull elements. These misinterpretations were readily corrected two years later (MEYER 1863) based on the new finds of *Nicrosaurus kapffi*. MEYER (1865b) presented what was then the only cranial reconstruction of *Nicrosaurus* species B based on the much more complete and less distorted BMNH 42745. Nevertheless, several key features of *Nicrosaurus* species B, most notably the shape of the temporal region, remained unknown or were not recognised in the material then available.

The taxonomic status of *Belodon plieningeri*, after 1861 clearly outlined and apparently well established, became heavily disrupted, when HUENE (1909, 1911) described the skull from Trossingen now considered the potential type of a new species, *Mystriosuchus* species B. He referred the specimen to *Belodon plieningeri* and combined the species name with the genus *Mystriosuchus*, thereby disregarding all contrary evidence from MEYER's specimens. This had a major impact not only on the status of the specimens of *Nicrosaurus* species B, but on the whole taxonomic concept of the European phytosaurs then known. In the first place, the distinction between *Mystriosuchus* and *Nicrosaurus* became hopelessly blurred. The then so heterogenously composed species *Mystriosuchus plieningeri* now included a specimen which virtually

invited arguments for a gradual transition between both genera (HUENE 1909, 1911; ABEL 1923). If more than one genus among European Norian phytosaurs was recognised, the referral of the Trossingen skull and MEYER's specimens of *Belodon plieningeri* to *Mystriosuchus* became common-place (CAMP 1930; CASE 1922, 1929, 1930; HUENE 1911, 1915, 1922, 1956; KUHN 1932, 1936, 1961b), though in doing so the nomenclatural principle of priority was fundamentally violated. Alternatively, since MEYER's specimens are clearly different from *Mystriosuchus*, but the Trossingen skull could hardly be referred to *Nicrosaurus*, the forced composition of *Belodon plieningeri* could only be maintained by a sort of compromise, in retaining the old genus-name *Belodon*, and so giving some sort of validity to this genus (e.g. WESTPHAL 1963b; 1976). Secondly, since a beautifully preserved and complete skull had been described in detail and hence the species characteristics of *Belodon plieningeri* seemed to be well established, there was obviously no need to consider MEYER's less complete specimens any more nor to describe any "inferior" specimen found afterwards. The specimen of *Mystriosuchus* species B soon became the reference specimen for the species *plieningeri* (= *Nicrosaurus* species B). The most important consequence, however, was that almost all subsequent workers in comparing other phytosaur taxa with *Belodon plieningeri* (= *Nicrosaurus*) actually compared them with a *Mystriosuchus*, leaving many of their conclusions necessarily distorted or invalid in a modern view (e.g. CASE 1922, 1929).

GREGORY (1962a) noted that the types of *Belodon plieningeri* are indeterminable, referred GPIT 261/001 to *Mystriosuchus*, and pointed out several similarities of the complete skulls of the remaining "*Belodon plieningeri*" to *Nicrosaurus kapffi*. However, he did not execute the taxonomic consequences, but retained the name "*Belodon plieningeri*" for the specimens. In later reviews, the name "*Belodon plieningeri*" is kept for the assemblage in the definition of the operational taxonomic unit of this study, i.e. "non-*kapffi*" *Nicrosaurus*, variably inclusive (WESTPHAL 1963b, 1976) or exclusive *Mystriosuchus* species B GPIT 261/001 (GREGORY & WESTPHAL 1969; LONG & MURRY 1995). HUNT (1994) was the first author to explicitly refer "*Belodon plieningeri*" to the genus *Nicrosaurus* in print.

2.3.2 Systematic palaeontology

Synonymy:

Nicrosaurus species B
(Figs. 2.45 - 2.64)

1859 gavialartiges Reptil – KAPFF: pp. 94, 95

1860 *Belodon Plieningeri* – MEYER [partim]: p. 212 "lange schmale Schnautze", non p. 212 "*Cylindricodon* JÄGER", "*Cubicodon* JÄGER" [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 212 "Hautknochen-Decke" [= *Paratypothorax andressi* LONG & BALLEW, 1985]. [1860a].

1860-61 vollständige Schädel – QUENSTEDT [partim]: p. 511, non p. 511 "Schilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1861 *Phytosaurus* – O. FRAAS [partim]: p. 101 [KAPFF's finds, partim], non p. 101 "Rübgarten" [= *Phytosaurus* JAEGER, 1828, *nomen dubium*], non p. 101 "Saurierreste von Löwenstein, Affalterach, Leonberg, Aixheim" [see MEYER (1847-55), PLIENINGER (1857), QUENSTEDT (1851-52)].

1861 *Belodon plieningeri* Meyer – MEYER [partim]: pp. 271, 346, pl. 28, pl. 29 figs. 1-5, 8-10, pl. 37 fig. 27, pl. 31 figs. 1-5, ? p. 346 " die meisten aus dem Rumpf untersuchten Knochen" [= Phytosauria indet.], non pp. 253, 346 "die meisten Kieferbruchstücke und Zähne" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*].

1862 *Belodon Plieningeri* – MEYER: p. 335.

1863 *Belodon Plieningeri* Meyer – MEYER: p. 241, pl. 42 fig. 6.

? 1863 junger *Belodon* – MEYER: p. 245, pl. 41 figs. 12-13.

1864 *Belodon Plieningeri* H. v. Meyer – ALBERTI [partim]: pp. 228, 229, non p. 228 [ref. to MEYER 1844, 1852-57, = *Belodon plieningeri* MEYER, 1844, *nomen dubium*].

1864 *Belodon Plieningeri* – MEYER: p. 210.

1865 *Belodon Plieningeri* – MEYER: p. 221. [1865a].

1865 *Belodon Plieningeri* Meyer – MEYER: pp. 100, 104, 110, pl. 23 figs. 1-2, pls. 24-26. [1865b].

1865-66 *Phytosaurus cylindricodon* – QUENSTEDT [partim]: p. 135 "*Belodon plieningeri*", non p. 133, pl. 9 fig. 1 [= *Nicrosaurus kapffi* (MEYER, 1860), modified after MEYER 1863], non fig. 46 [= *Phytosaurus cubicodon* JAEGER, 1828, nom. dub.], non p. 134, fig. 47 [= *Mystriosuchus planirostris*

(MEYER, 1863)], non p. 134 "Schilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1870 *Belodon* – HUXLEY [partim]: pp. 39, 40.

1872 *Phytosaurus Plieningeri* – SCHEMPP: p. 212.

1877 Saurierreste – O. FRAAS [partim]: p. 2.

1887 *Belodon Plieningeri* – KOKEN: p. 404.

1887-90 *Belodon plieningeri* H. v. Meyer – ZITTEL: pp. 640, 643, fig. 563 left centre [modified after MEYER (1865b)].

1888 *Phytosaurus plieningeri* (Meyer 1842) – LYDEKKER: p. 128.

1896 *Belodon Plieningeri* V. MEY. – E. FRAAS: p. 16.

1906 *Phytosaurus pleiningeri* [sic] (H. VON MEYER, 1842) – MCGREGOR [partim]: pp. 37, 39, 40, 44, 47, 49, 51, 59, 93, non pp. 31, 93 "*Belodon pleiningeri*" [sic] [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*].

1907 *Belodon Plieningeri* – ESER: p. 660, ? p. 661 [jaw fragments from Wangen in ESER's collection].

1907 *Phytosaurus plieningeri* – LEES: pp. 146, 142.

1908 *Belodon Plieningeri* H. v. MEY. – ENGEL [partim]: pp. 172, 170.

1909 *Phytosaurus Plieningeri* H. v. MEYER sp. – HUENE [partim]: pp. 586, 592, non p. 583, non figs. 1, 5-7 [= *Mystriosuchus* species B].

1910 *Belodon* (*Phytosaurus*) *Plieningeri* H. v. MEY. – E. FRAAS: p. 23, ? p. 23 [postcrania, Phytosauria indet.].

1910 *Belodon*-Reste – LANG [partim]: p. 50 footnote 1.

1911 *Mystriosuchus Plieningeri* H. v. MEYER sp. – HUENE [partim]: p. 88, pl. 15, figs. 10-11, non pp. 68, 91, non pls. 12-14, non pl. 17 fig. 7, non figs. 2-9 [= *Mystriosuchus* species B].

1913 *Belodon Plieningeri*– E. FRAAS: p. 1097. [1913a].

1913 *Mystriosuchus plieningeri* – E. FRAAS: p. 275. [1913b].

1914 *Belodon Plieningeri*– E. FRAAS: p. 126.

1915 *Mystriosuchus plieningeri* – HUENE [partim]: p. 491 [includes *Mystriosuchus* species B]. [1915a].

1915 *Belodon* (*Mystriosuchus*) *plieningeri* H. von Meyer sp. 1842 – MEHL [partim]: pp. 162, 150, non pp. 144, 147 [= *Mystriosuchus* species B].

1922 *Mystriosuchus Plieningeri* H. v. MEYER – HUENE [partim]: pp. 60, 86 "von H. v. MEYER abgebildetes Exemplar", 88, 146, non p. 146 "*M. ingens* E. FRAAS" [= *Belodon ingens* E. FRAAS, 1896. *nomen nudum*], non pp. 60 "großer Schädel", 67, 87, 99, 100 [= *Mystriosuchus* species B].

1923 *Phytosaurus Kapffii* [sic] MEYER – ABEL [partim, "*Mystriosuchus Plieningeri*" H. v. MEY.]: pp. 26, 44 "unter dem Namen *Belodon Plieningeri*

MEY. beschriebene Schädel", 45 "Nr. 42745", non pp. 30, 31, 44 "der Tübinger Sammlung", 45 "längere Schädel", fig. 1 [= *Mystriosuchus* species B].

1928 *Mystriosuchus Plieningeri* H. v. MEYER sp. – SCHMIDT [partim]: p. 418 "Symphyse des Unterkiefers", fig. 1172a lower jaw [cop. HUENE 1911], non figs. 1172a, 1172b [= *Mystriosuchus* species B].

1928 *Phytosaurus kapffi* H v. MEYER – SCHMIDT [partim]: fig. 1165a [cop. MEYER 1861, non cop. JAEGER 1828], ? figs. 1165b, 1167 [postcrania cops. HUENE 1902, 1922, = Phytosauridae indet.],, non p. 415 [= *Belodon ingens* FRAAS, 1896, *nomen nudum*], non p. 415 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*], non p. 415, non fig. 1166 [= *Nicrosaurus kapffi* (MEYER, 1860), modified after FRAAS 1896] non p. 415 figs. 1165a, 1169 [= *Phytosaurus cubicodon* JAEGER , 1828, *nomen dubium*], non fig.1168 [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1929 Parasuchierschädel – STOLL: pp. 47, 15.

1929 Belodon-Knochen – STOLL [partim]: p. 41.

1930 *Mystriosuchus plieningeri* – CAMP [partim]: pp. 140 "more slender forms", 141 "later descriptions", fig. 6 "27.5%", non pp. 140, 141 von Meyer (1844: p. 44, pl. 12, figs. 20, 21) [= *Belodon plieningeri* MEYER, 1844], non fig. 6 "33,3%" [= *Mystriosuchus* species B].

1930 *Mystriosuchus pleiningeri* [sic] – CASE: p. 161.

1932 *Mystriosuchus plieningeri* H. v. M. – KUHN: p. 122.

? 1932 *Mystriosuchus* cf. *plieningeri* H. v. M. – KUHN: pp. 95, 121, 122, fig. 4 [= Phytosauria indet.].

1933 *Mystriosuchus plieningeri* H. v. Meyer 1842 sp. – KUHN [partim]: p. 20-21.

? 1933 *Mystriosuchus* spec. nov.? – KUHN: p. 21 [= Phytosauria indet., see KUHN (1932)].

1934 *Mystriosuchus plieningeri* – KUHN: p. I.

1936 *Mystriosuchus plieningeri* H. v. Meyer – KUHN [partim]:, p. 92, non p. 89 [humerus, = Phytosauria indet.].

? 1936 *Mystriosuchus* cf. *plieningeri* H. v. Meyer – KUHN: pp. 91-92 [= Phytosauria indet.].

? 1938 *Mystriosuchus* cf. *plieningeri* H. v. M. – KUHN: pp. 318, 319

non 1954 *Mystriosuchus plieningeri* – HELLER: p. 10 [= *Mystriosuchus* species B].

1956 *Mystriosuchus plieningeri* – HUENE [partim]: p. 463, non fig. 496a-b [= *Mystriosuchus* species B; cop. HUENE 1911, relettered].

1961 *Mystriosuchus plieningeri* (H. v. Meyer 1842) – KUHN [partim]: p. 95. [1961b].

1962 *Belodon plieningeri* Meyer, 1842 – GREGORY [partim]: p. 676 "slender-snouted specimens", 677 "in Meyer's collection", p. 663 tab. 1, non p. 675, 676, 677 "type specimens" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non p. 677 "Trossingen skull" [= *Mystriosuchus* species B]. [1962a].

1963 *Belodon plieningeri* – WESTPHAL [partim]: fig. 3, non fig. 5 top [= *Mystriosuchus* species B]. [1963a].

1963 *Belodon plieningeri* H. v. MEYER – WESTPHAL [partim]: pp. 161, 162, 163 "Zähne, Unterkiefer MEYER (1965: pls. 46-47)", 164 "Squamosum", non p. 162 "Meyer 1844: pl. 20 figs. 20-24, 18-19" [= *Belodon plieningeri*, MEYER, 1844, *nomen dubium*], non pp. 163 "Rostrum", 164 "Schädelbreite, -höhe, -skulptur", fig. 1 top [= *Mystriosuchus* species B]. [1963b].

1963 *Belodon plieningeri* H. v. MEYER 1844 – WESTPHAL : p. 22. [1963c].

? 1966 *Mystriosuchus plieningeri* VON MEYER – DUTUIT: p. 30.

1969 *Belodon plieningeri* – GREGORY [partim]: pp. 44, 46, non p. 44 "Typus-Exemplare" [= *Belodon plieningeri*, MEYER, 1844, *nomen dubium*].

1969 *Belodon plieningeri* Meyer 1844 – GREGORY & WESTPHAL [partim]: pp. 1296 "skull from Pfaffenhofen", 1297 "from the Stuttgart area", non pp. 1296, 1297 "type material" [= *Belodon plieningeri*, MEYER, 1844, *nomen dubium*].

1971 *Belodon plieningeri* MEYER 1842 – KUHN [partim]: p. 14, ? fig. 24(9) [osteoderms, cop. WESTPHAL 1970], non figs. 24(3), 25(2-3) [= *Mystriosuchus* species B].

1973 Phytosaurier – BRENNER [partim]: p. 171 "Pfaffenhofen", "Kayh", non p. 171 "Trossingen" [= *Mystriosuchus* species B].

1976 *Belodon plieningeri* H. v. MEYER 1844 – WESTPHAL [partim]: p. 111 "breiter Postorbitalsteg, Hinterschädel, Zähne, Skulptur", fig. 8e, ? p. 111 "dorsaler Panzer", fig. 8d [= Phytosauria indet.], non p. 111 "Typus-Material" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non p. 111 "Wucherungen, Squamosum" [= *Mystriosuchus* species B], non p. 111 "B. ingens E. Fraas 1896" [= *Belodon ingens* E. Fraas, 1896, *nomen nudum*].

1978 (Saurier-) Reste – BRENNER [partim]: p. 136. [1978a].

1982 *Belodon plieningeri* Meyer 1844 – BUFFETAUT & INGAVAT [partim]: p. 10 "figured by H. von Meyer (1861, pl. XXIX, fig. 1)", non fig. 1A [= *Mystriosuchus* species B].

1985 *Belodon plieningeri* – LONG & BALLEW: p. 86.

? 1989 "*Mystriosuchus* aff. *plieningeri* Meyer" – WILD: p. 16 footnote [= Phytosauria indet.].

1992 *Mystriosuchus planirostris* – SERENO & WILD: p. 436.

1993 *'Belodon'* – BENTON & WILD [partim]: p. 37.

1993 *Mystriosuchus* – BENTON & WILD: p. 37.

1994 *Nicrosaurus* n. sp.– HUNT: p. 30A.

1994 Saurierknochen – JUNGHANS [partim]: p. 57.

1995 *Belodon plieningeri* – HUNGERBÜHLER [partim]: p. 70 "neugefundene Schädel", non p. 70, fig. 4 [= *Mystriosuchus* species B], non p. 70 "Phytosaurierzähne" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*].

1995 Pseudopalatinae gen. et sp. indet. resembling *Pseudopalatus* – LONG & MURRY: p. 62, figs. 40D, 56C.

1997 "*Belodon*" *plieningeri* – GODEFROIT & CUNY: p. 7.

1997 *Phytosaurus cylindricodon* – WITMER [partim]: p. 17 "BMNH 38039", non p. 17 "BMNH 38040" [= rauisuchian cf. *Teratosaurus suevicus* MEYER, 1861].

1997 *Phytosaurus* sp.– WITMER [partim]: p. 48 "BMNH 38039", non p. 48 "BMNH 38040" [= rauisuchian cf. *Teratosaurus suevicus* MEYER, 1861].

Referred specimens:

(1) Skulls and skull fragments:

SMNS 12593: complete skull lacking the mandible (Figs. 2.47 - 2.54). For measurements, see Table 2.3.1. "Werkstein"-beds, quarry "Weißer Steinbruch", Pfaffenhofen (Fig. 1.1); middle Stubensandstein, subunit sc1 (see Appendix C, 2).

SMNS 4059: badly distorted skull lacking the braincase, occipital and temporal region, and the right cheek (MEYER 1861: pl. 28, pl. 29 figs. 1-5; Figs. 2.45 - 2.46). For measurements, see Table 2.3.1. Heslach.

BMNH 42745: largely undistorted skull, but with severe post-recovery damages to the cheeks, the pterygoids, the temporal region, and the whole dorsal surface. A fragment of the right squamosal body including the paroccipital process of the squamosal is preserved separately among numerous other tiny fragments derived from this specimen (MEYER 1865b: pls. 24-26; HUENE 1911: pl. 15; Figs 2.55 - 2.59). For measurements, see Table 2.3.1. Heslach or Kaltental.

GPIT 2070.001: skull lacking most of the postorbital part (WESTPHAL 1963a: fig. 3; Figs. 2.60 - 2.62). For measurements, see Table 2.3.1. Kayh near Tübingen (Fig. 1.1), middle Stubensandstein, subunit sc2 (see Appendix C, 9).

Table 2.3.1: *Nicrosaurus* species B, cranial measurements.

All measurements are in mm. The specimens are ordered in accordance with skull length. The numbers 1 - 24 correspond to the distances illustrated in Figure 2.2.

character	SMNS 12953	SMNS 4059	BMNH 42745	GPIT 2070.001
1 skull length overall	610	650 (est.)	683 (est.)	715 (est.)
2 distance tip of snout - basioccipital condyle	560	650[1]	630	indet.
3 distance tip of snout - anterior corner of antorbital fenestra	390	410	430	442 (s)
4 distance tip of snout - anterior corner of naris	375	400	420	440
5 distance tip of snout - anterior rim of orbit	465	505	530	545
6 distance tip of snout - anterior corner of infratemporal fenestra	480	indet.	535 / 540	indet.
7 distance between orbit and naris	indet.	55	indet.	64
8 maximum width quadrate - quadrate	191	indet.	215	indet.
10 height quadrate - skull roof	63	102	105	89[2]
11 width of snout at anterior constriction	21	24	30.5	31.5
12 width of snout at posterior constriction	–	indet.	indet.	40.5
13 width of skull roof	46	indet.	57	indet.
14 width of postorbito-squamosal bar	29.5	indet.	32.5	32
15 length of postorbito-squamosal bar	93.7	indet.	indet.	indet.
17 length of posterior process of squamosal	22	indet.	indet.	indet.
18 axial diameter of orbit	48.7 (d)	58	54.3 (d)	54 (s)
19 transverse diameter of orbit	33 (d)	46	39.3 (d)	50 (s)
20 width of supratemporal fenestra (anterior rim)	9.2	indet.	(13)	indet.
23 width of posttemporal fenestra	21	indet.	indet.	indet.
24 height of posttemporal fenestra	5.1	indet.	8.5	indet.
thickness of postorbito-squamosal bar at anterior corner of infratemporal fenestra	9	indet.	10	13
depth of palatal vault	19	30	34	25

[1] for preservational reasons, the distance between the tip of snout and the quadrate

[2] for preservational reasons, the distance between the skull roof and the basal tubera

Symbols and abbreviations:

( ) = minimal value given because of incomplete preservation; / = left side / right side; – = not present in specimen; (d) = dexter, right; (est.) = estimated according to measurement (4); indet. = indeterminable, mostly because of incomplete preservation; (s) = sinister, left.

SMNS 12593/2: strongly laterally compressed skull fragment lacking most of the rostrum and the whole postorbital part. "Werkstein"-bed, quarry "Weißer Steinbruch", Pfaffenhofen; middle Stubensandstein, subunit sc1 (see Appendix C, 2).

SMNS uncat. no. 11: fragmentary left half of a snout (Figs. 63 - 64). The specimen consists of the narial region with the prenarial crest, and the tip of a snout, which were incorrectly assembled in KAPFF's times resulting in a shortening of the snout for a distance of 10 alveoli (corresponds approximately to 100 mm). The specimen was restored recently, but left in its original incorrect association (R. WILD, pers. com., 1997). While the posterior fragment is clearly *Nicrosaurus* species B, the anterior piece is only tentatively referred to the species, under the assumption that it belongs to the same specimen. Heslach or Kaltental.

BMNH 38039: left half of a snout lacking the tip (MEYER 1864: 211; MEYER 1865b: 110-112). Heslach or Kaltental.

(2) Mandibles:

No mandible was ever found articulated or even in association with a skull of *Nicrosaurus* species B. The following complete specimens are referred to the species based on the lesser length of the mandible and width of the glenoid facet than mandibles found associated with *Nicrosaurus kapffi*, which is supported by features of the dentition, the alveolar size, and the alveolar spacing corresponding to the skull material. The mandible of *Mystriosuchus planirostris* is distinguished by a proportionally longer symphysis (subsection 3.2.2).

BMNH 38038: right mandibular ramus with an almost complete dentition (MEYER 1865b: pl. 23; LONG & MURRY 1995: fig. 56C). For measurements, see Table 2.3.2. Heslach or Kaltental.

GPIT 261/011: right mandibular ramus with some anterior teeth preserved in place (HUENE 1911: fig. 11). For measurements, see Table 2.3.2. The provenance of the specimen is unknown, though HUENE (1911) suggested Heslach on the base of the mode of preservation.

Table 2.3.2: *Nicrosaurus* species B, mandible measurements (in mm).

character	BMNH 38038	GPIT 261/011
total length	634	630
length of symphysis (% of total length)	313 (49%)	290 (46%)

Additionally, numerous slender fragments of mandibular rami and snouts from the Stuttgart area are kept in the collections in Stuttgart (SMNS 54707 [MEYER 1861: pl. 31 fig. 1-5], SMNS uncat. nos. 2 [MEYER 1861: 280-281], 3 [MEYER 1861: pl. 41 fig. 12-13], 6 [MEYER 1861: pl. 37 fig. 32], and 8 [MEYER 1861: pl. 29 figs. 8-10; PLIENINGER 1857: pl. 8 fig. 2]), Tübingen (mandible fragment GPIT uncat. no. 400), and in the former collection A. KRUPP now housed in the Ruhrlandmuseum Essen (two dentary fragments RME Re 551.761.3 A037/1 and 037/2). The provenance of these specimens suggests *Nicrosaurus* species B, but all incomplete rostra cannot be safely distinguished from *Mystriosuchus planirostris* on the basis of anatomical differences. For this reason, they are not referred to a particular species.

(3) Postcrania: None.

Summary description: moderate-sized (skull = 600 - 700 mm in length), gracile, and slender-snouted species of *Nicrosaurus*; prenarial crest may be present over posterior part of the snout; septomaxilla terminates at the level of the anterior tip of the nasal; narial wing frequently present and anterior part of the internasal septum prominent and visible in lateral view; posterior part of the naso-septomaxillary suture forms a deep groove in front of the nares; sculpture of the preorbital region prominent; maxillo-nasal suture enters the antorbital fenestra; lateral face of the maxilla subvertical; cheek region (quadratojugal and jugal) with a well developed longitudinal depression; ventral edge of the quadratojugal-jugal bar thin and sharp; craniomandibular facet of the quadrate less wide than in *Nicrosaurus kapffi*, lateral condyle offset from the cheek; postorbito-squamosal bar broader in relation to *Nicrosaurus kapffi*; dorsal rim of the squamosal process of the parietal gently sloping and posteromedially deflected over the supraoccipital shelf leading to an occipitally facing groove; lateral body of the squamosal high in relation to *Nicrosaurus kapffi*; length of the squamosal body increased resulting in a wider tympanic fossa; quadratojugal process of the squamosal extends along more than the half of the infratemporal fenestra; in dorsal view, the posterior process of the squamosal is continuously broad, the medial rim is angular and not significantly thickened; posterior process of the squamosal terminates with a pointed tip, and no ventrally pointing knob present; paroccipital process of the squamosal small; supraoccipital shelf long anteroposteriorly; base of the paroccipital process comparatively expanded, dorsoventrally compressed with a strong posterior ridge; extremity of the paroccipital process strongly compressed anteroposteriorly; supraoccipital borders the foramen magnum; opisthotic lamella between the stapedial and the jugular groove low, blunt, and thick; alveolar ridges more prominent than in *Nicrosaurus kapffi*; prechoanal part of the vomers mostly slender and tapering; both grooves on the pterygo-quadratal bar

weakly developed or absent; ridge on the anteriormost lateral border of the pteroccipital fenestra; basal tubera formed mostly by the basisphenoid, elongated transversely, and face more posteriorly than in *Nicrosaurus kapffi*; basisphenoid corpus constricted; upper jaw dentition bipartite; premaxilla teeth set more laterally than in *Nicrosaurus kapffi*; symphysis equals c. 50% of the total mandibular length.

Diagnosis: dorsolateral thickness of postorbito-squamosal bar reduced to c. 10 mm (i.e. half the value of *Nicrosaurus kapffi*).

Distribution: in central Württemberg Heslach near Stuttgart and Kayh near Tübingen; Pfaffenhofen in northern Württemberg (Fig. 1.1).

Stratigraphic range: Upper Triassic, Keuper succession, Middle Keuper, Stubensandstein, middle Stubensandstein, based on SMNS 12593, SMNS 12593/2, and GPIT 2070.001. The occurrence in the lower Stubensandstein of Heslach, which was postulated by WILD (1991) and BENTON & WILD (1993), cannot be assessed on the basis of the data preserved with the specimens and needs to be confirmed by new finds (see discussion in Appendix C, 4.2).

Age: Early (to Middle?) Norian, Late Triassic.

2.3.3 Description

As far as preserved in the specimens, there are no fundamental osteological differences between *Nicrosaurus* species B and *Nicrosaurus kapffi*. Thus, it is not necessary to present an exhaustive osteology of *Nicrosaurus* species B here. The description will focus on the SMNS 12593, which provides long-missing anatomical data mainly on the temporal region, and on character states differing from *Nicrosaurus kapffi*. No information is available at present on the lateral and anterior aspect of the braincase.

Snout

Sculpture. The skull roof, the orbitonasal and the narial region are generally more strongly sculptured than in *Nicrosaurus kapffi* (see SMNS 4059: MEYER 1861: pl. 28; SMNS 12593: Fig. 2.47). The ornamentation of the skull roof consists of a mosaic of irregular blunt ridges separated by pits and undulating grooves. In the preorbital part of

the face, the sculpture is even better developed. In particular the flank of narial bulb, i.e. the area surrounded by the orbit, the naris, and the antorbital fenestra, is ornamented with prominent blunt knobs; here, the grooves are lacking and the concave component of the ornamentation includes only narrow and deep pits. *Nicrosaurus* species B also shows far more numerous foramina at tip of snout (SMNS 4059, BMNH 42745: Fig. 2.55).

Snout shape and premaxilla crest. The anterior part of the snout is semicircular in diameter: in two specimens it has a dorsoventrally flattened surface (SMNS 12593: Fig. 2.52, GPIT 2070.001: Fig. 2.62). A slight hump in the middle of the premaxilla is present in all specimens (BMNH 42745: Fig. 2.57, SMNS 4059: MEYER 1861: pl. 29 fig. 2, to a lesser degree in GPIT 2070.001: Fig. 2.62) except SMNS 12593, in which a convexity might be obscured by the considerable degree of compression of the snout. Such a raised snout area has been reported as being common in other slender-snouted phytosaur taxa (CASE 1922, 1929; see CASE & WHITE 1934 for an actual specimen). An unique feature among specimens of *Nicrosaurus* is present in the anterior part of SMNS uncat. no. 11 (Fig. 2.63). In this specimen, the hump is developed into a sharp premaxilla crest. The crest starts dorsally above alveolus pm (5), ascending for a distance of 40 mm to reach a maximum height with 15 mm over the dorsal snout surface at the level of pm (9). The premaxilla crest remains horizontal for at least another 60 mm, until it is cut off by the broken end of the fragment. The sutural contact between the premaxillae and septomaxillae, preserved in SMNS uncat. no. 11 in medial aspect, is in contrast to *Nicrosaurus kapffi* SMNS 54708 not smooth and undulating, but a plain roughened articular surface. The orientation of the bony fibres can be traced as fine superficial striations (Fig. 2.64). The maximum thickness of only 19 mm at the basis of the crest in this specimen (resulting in a depth of 38 mm for a complete crest) suggests that the prenarial crest in *Nicrosaurus* species B represents a massive rather than internally cavernous structure.

Presence and shape of a prenarial crest: The majority of specimens (SMNS 12593, BMNH 42745, BMNH 38039, and GPIT 2070.001) show a gently sloping prenarial snout section that descends at a maximum angle of 20°, and a transversely rounded snout profile. The latter corresponds to the snout profile of most uncrested phytosaurs, and I regard this shape as the primitive condition.

The snout shape of these specimens is contrasted by a high, steep and sharp prenarial crest in SMNS 4059 (MEYER 1861: pl. 28) and SMNS uncat. no. 11, the crest being almost knife-like in its anterior part in the latter. However, the shape of the prenarial crest is not uniform. While the prenarial crest of SMNS 4059 slopes gradually in front of the naris as the rostrum in the uncrested specimens, the crest is more

distinguishable in SMNS uncat. no. 11 (Fig. 2.63). It starts 50 mm in front of the nares, following a gradual decline of the snout profile. The prenarial crest itself is of parabolic shape with a steep anterior descent until the crest merges with the slender snout at a point on the level of the premaxilla-maxilla suture. The prenarial crest is sculptured in both specimens with fine undulating lineations, very distinct from the ornamentation of the narial region. The medial view of SMNS uncat. no. 11 (Fig. 2.64) demonstrates, that the prenarial crest in *Nicrosaurus* species B is a massive, non-pneumaticised structure.

An intermediate condition is found in GPIT 2070.001 and SMNS 12593: the dorsal part of the area immediately in front of the nares is slightly narrower than the base of the rostrum, while being still well rounded, and is set off by two shallow grooves confluent with the infranasal recess (Figs. 2.47, 2.60). Because of the peculiar crater-like nares of GPIT 2070.001, there is an abrupt and steep descent of the snout profile in this specimen, followed by a slight prenarial hump and a gradual decline to a flat angle (Fig. 2.62).

Nares. In SMNS 12593 and BMNH 42745, the nasal opening ends in an elongated and pointed anterior tip, which continues into a short groove along the naso-septomaxilla suture (Figs. 2.47, 2.55). The shape of the narial rim is dimorphic in *Nicrosaurus* species B. An excavation of the anterior rim of the naris creates a distinct step of the rim, as in *Mystriosuchus*, behind a triangular, flat plane (SMNS 4059: Fig. 2.45, SMNS 12593: Fig. 2.47, BMNH 42745: Fig. 2.55). The posterior flank of the naris posterior to the step is introduced here as a narial wing. The narial rim in the other specimens (GPIT 2070.001: Fig. 2.62, BMNH 38039, SMNS uncat. no. 11: Fig. 2.63) is undulating and gently sloping anteroventrally over the whole length with an average slope of about 15°. The nasal opening of GPIT 2070.001 is peculiar in showing a steep vertical nasal crater, which results in a marked concave orbitonasal region in this specimen.

Nicrosaurus species B can be safely distinguished from other slender-snouted phytosaurs by the well marked infranasal recess reaching from the level of the narial wing along the anterior third of the antorbital fenestra and extending forward beyond the nares (Figs. 2.52, 2.57, 2.62, somewhat obscured in GPIT 2070.001 because of crushing). This accounts for the offset condition of the broadly rounded prenarial "crest" in SMNS 12593 and GPIT 2070.001. In SMNS 12593, the infranasal recess is most conspicuously deep, which results in a marked overhang of the anterior narial rim over the flank of the snout with steeply inward sloping flanks. The infranasal recess does not extend along the posterior part of the nares as in some *Nicrosaurus kapffi*, but is cut off by the outward bulging narial bulb.

The anterior part of the internarial septum is bulging and elevated over the narial rim, but never rectangular in shape, as in *Mystriosuchus planirostris* (BMNH 42745: Fig. 2.57, partially broken off in SMNS 12593: Fig. 2.52). The visibility in lateral view is clearly a result of the anterior excavation of the narial rim leading to the narial wing. In GPIT 2070.001, on the contrary, the internarial septum is depressed relative to the rim of the naris, the highest point being at mid-length. It is obvious from SMNS uncat. no. 11, that the septum is entirely formed by the septomaxilla (Fig. 2.64). A discrete vertical lamella of bone covers the lateral flank of the internarial septum in SMNS 12593 (Fig. 2.52: right side, left side obscured by matrix), and runs in a parabolic course to disappear in the anteromedial tip of the naris. It cannot be established whether the bone is a separate ossification or a process rising dorsally from an underlying element like the vomer or the pterygoid.

Septomaxilla. The septomaxilla terminates anteriorly at the level of the tip of the nasal about 50 mm in front of naris (BMNH 42745: Figs. 2.55, 2.57, SMNS uncat. no. 11: Fig. 2.63). The dorsal surface of the bone is slender with one tapering prong wedged between the premaxillae (BMNH 42745, SMNS 12593: Fig. 2.47), the condition described as state A in *Nicrosaurus kapffi* (part 2.2.3.3). In SMNS 12593 and BMNH 42745, the septomaxillae are broadened in the anterior section of the internasal septum because of the pointed external nasal openings. The reconstruction of BMNH 42745 by HUENE (1911: fig. 10), in which the premaxilla and the nasal meet between and underneath both septomaxillae, cannot be completely rejected for the specimen, but is unlikely to apply in general. Since the sutures identified by HUENE are situated in a superficially eroded area in front of the nares, it is impossible to corroborate their presence with any degree of confidence. However, the snout halves SMNS uncat. no. 11 and BMNH 38039 show a large and continuous interseptomaxillary joint surface (Fig. 2.64). Likewise, in *Smilosuchus* the septomaxillae are joined along the median plane all the way down to the prenarial cavity and only in the anteriormost part, do the septomaxillae begin to diverge ventrally (CAMP 1930: figs. 22, 25).

Maxilla. The maxilla is a high and slender bone, and the entire external surface slopes steeply ventrolaterally. There is no maxillary shelf or flange developed as in the robust morph of *Nicrosaurus kapffi*, and consequently the antorbital fenestra opens dorsolaterally to laterally in all specimens. Although the configuration of the narial region is somewhat difficult to reconstruct because of the extensive sculpturing, the maxillo-nasal suture is most likely to enter the antorbital fenestra in SMNS 12593, BMNH 42745, and SMNS uncat. no. 11 (Figs. 2.52, 2.57, 2.63).

Antorbital fenestra. The antorbital fenestra of *Nicrosaurus* species B is equipped with well developed internal laminae. Especially in SMNS 12593, there is a well developed lamina spanning the posterior antorbital cavity (Figs. 2.47, 2.52). The presence of an internal antorbital lamina is coupled with a narrow and pointed posterior rim of the opening. A comparatively broad lamina is also present along the dorsal rim. Both these laminae are formed by the lacrimal, and the lacrimo-nasal suture runs partially along the internal dorsal rim of the antorbital fenestra (Fig. 2.52). An internal antorbital opening has only been reported for non-phytosaurid phytosaurs and *Angistorhinus* so far and is reduced in more derived taxa. The presence of this feature in at least one specimen of *Nicrosaurus* species B is a plesiomorphic feature.

Skull roof

Orbits. *Nicrosaurus* species B show the same differences regarding orbit orientation as already noted for the morphs of *Nicrosaurus kapffi*: in low-domed specimens (SMNS 12593, GPIT 2070.001), the orbital plane is at lower angle to the skull roof than in high-domed specimens (SMNS 4059, SMNS 12593/2, BMNH 42745). However, in both morphs of *Nicrosaurus* species B the orbits face generally more to the side and less upward than in their counterparts of *Nicrosaurus kapffi*. Features not present in *Nicrosaurus kapffi* are the strongly dorsolaterally protruding orbital rims, which can be raised to prominent longitudinal ridges (SMNS 4059: MEYER 1861: pl. 29 fig. 2, GPIT 2070.001: Fig. 2.60). The orbits thus enclose an interorbital depression (BMNH 42745, GPIT 2070.001), and in GPIT 2070.001 the median sutures of the skull roof are elevated and ridge-like as well (Fig. 2.60).

Postorbito-squamosal bar. The postorbito-squamosal bar is stouter and thus somewhat stronger expanded medially in SMNS 12593 (Fig. 2.48A) compared with BMNH 42745 (Fig. 2.55) and most specimens of *Nicrosaurus kapffi*. The width-to-length ratio of the specimen still falls within the range of *Nicrosaurus kapffi* (e.g. SMNS 4379). The postorbito-squamosal bar in *Nicrosaurus* species B is, however, comparatively much thinner than in *Nicrosaurus kapffi* (SMNS 12593: Fig. 2.48B, BMNH 42745). BMNH 42745 shows a slight lateral ridge of the squamosal above the infratemporal fenestra (Fig. 2.57), which is reminiscent of the lateral squamosal ridge in *Mystriosuchus* and non-phytosaurid phytosaurs.

Temporal region

SMNS 12593 is the only specimen which provides information on the whole temporal region by combining the evidence from the preserved sections of the left and right side, and the core of the description is based on this specimen and illustrated in the Figures. 2.48, 2.53, and 2.54. Some additional data on single characters, especially the sutural configuration, is available from BMNH 42745.

Parietal. As illustrated in Figure 2.48, the squamosal process of the parietal is oriented posterolaterally at an angle of c. 30° to the longitudinal axis of the skull. The slope of the dorsal edge of the process toward the opisthotic was probably much gentler than in *Nicrosaurus kapffi*. The actual angle to the horizontal plane is difficult to assess, since the medial part of the parietal lamella is missing in SMNS 12593. The relative height of the parietal lamella is the main reason for the reduced width of the supratemporal fenestra. It is also evident that the parietal process probably overhangs the supraoccipital shelf to a much greater degree than in *Nicrosaurus kapffi*. Although the dorsal part of the lamella in the specimen is broken and somewhat pushed downwards and projects as a steep lateral ledge over the supraoccipital shelf, the thin lateral part of the process clearly forms a ridge that overhangs the underlying supraoccipital and the parietal process of the squamosal. The overhang continues into a concave, posteriorly facing area of the process under the medial half of the supratemporal fenestra, that effectively forms a groove (Fig. 2.54). In *Nicrosaurus kapffi*, the height of the squamosal process diminishes more rapidly and reaches the state of a flat tongue at a point more medially; consequently a distinct groove is not developed. The part of the squamosal process of the parietal of BMNH 42745 extending onto the supraoccipital (Fig. 2.54, right-hand side) compares to the deepest lamina seen in specimens of *Nicrosaurus kapffi* . The significant size is confirmed by SMNS 12593, in which a much greater area of the posterior part of the shelf is covered than in *Nicrosaurus kapffi*, and the squamosal process even extends over the posterior edge of the supraoccipital shelf into the recess leading to the corner of the posttemporal fenestra (Fig. 2.54). The squamosal process is excluded from the posttemporal fenestra in both specimens, which suggests that this might also be the case in *Nicrosaurus kapffi*. Laterally, the parieto-squamosal bar continues gradually into a thin but wide bar. The squamoso-parietal suture is placed laterally from the middle of the parieto-squamosal bar and hidden under the overhang of the squamosal (Fig. 2.48).

Squamosal. The squamosal of SMNS 12593 is definitely proportionally longer than in *Nicrosaurus kapffi*. While there is no difference in the length of the posterior process overhanging the paroccipital process of the opisthotic (Tab. 2.3.1), the length of the squamosal body between the posterior corner of the infratemporal fenestra and the

paroccipital process is enhanced by means of the wider tympanic fossa (Fig. 2.53). The same condition is also present in BMNH 42745 (Fig. 2.57). Thus, the squamosal extends actually more posteriorly beyond the level of the craniomandibular joint of the quadrates and, for this reason, appears to be more slender. It is, however, difficult to express the elongation in absolute terms that can be estimated significant. Moreover, the slenderness of the temporal region in *Nicrosaurus* species B is pronounced by the reduced supratemporal fenestrae, the medial rims of the squamosal diverging to a lesser degree, and the elongated supraoccipital shelf (Figs. 2.47, 2.55). Regarding the actual width of the posterior process and postorbito-squamosal bar, both *Nicrosaurus* species are not markedly dissimilar (Tabs. 2.2.1, 2.3.1). SMNS 12593 is the only specimen that can give insight into the shape of the posterior process of the squamosal in *Nicrosaurus* species B (Fig. 2.47). The medial rim is slightly divergent. Toward the extremity, the squamosal rim turns outward at an angle to terminate in a well pointed tip (see Fig. 2.49). The medial rim is somewhat thickened, but not to such a degree as in *Nicrosaurus kapffi*, and because of the thin medial flange of the squamosal there is no flattened area present on the posteromedial rim (Fig. 2.48). The ventral surface of the squamosal (Fig. 2.54) shows the same sulci and recesses as *Nicrosaurus kapffi*, and there are only insignificant differences in SMNS 12593 in comparison to *Nicrosaurus kapffi* (Fig. 2.11). The ventral recess is less narrow because of a more horizontal orientation and therefore flatter parieto-squamosal bar. SMNS 12593 also lacks the well developed knob at the extremity of the posterior process seen in all *Nicrosaurus kapffi*, and this results in a poorly defined triangular recess (Fig. 2.48).

The parietal process of the squamosal extends underneath the squamosal process of the parietal to meet the supraoccipital, and together squamosal and supratemporal form the entire dorsal margin of the posttemporal fenestra (BMNH 42745: Fig. 2.59). While the squamosal borders the posttemporal fenestra laterally as well, there is no evidence for a lamina covering the paroccipital process and approaching the fenestra from ventrally (Fig. 2.54).

The quadratojugal process of the squamosal is visible for a longer distance along the posterior rim of the infratemporal fenestra, forming at least the upper half of the border (Figs. 2.53, 2.57).

Supratemporal opening. The shape of the supratemporal fenestra varies considerably in the specimens referred to *Nicrosaurus* species B. The supratemporal fenestra cuts less far into the skull roof in *Nicrosaurus* species B than in *Nicrosaurus kapffi*. The anterior rim is round in SMNS 4059 (Fig. 2.45), BMNH 42745 (Fig. 2.55), and GPIT 2070.001 (Fig. 2.60), which all correspond to *Nicrosaurus kapffi* regarding this character. The first mentioned specimen shows a somewhat laterally compressed,

oval outline of the fenestra. This contrasts markedly with SMNS 12593, in which the anterior rim of the supratemporal fenestra is angular, and even notched anterolaterally (Fig. 2.48).

In SMNS 12593, the supratemporal fenestra is considerably smaller than in *Nicrosaurus kapffi*. This is evident especially in the posterior part of the opening. Because of the gently rather than steeply sloping edge, the squamosal process of the parietal closely approaches the median extension of the squamosal, and the fenestra is drastically reduced in width. Here, the opening is merely a slit between the parieto-squamosal bar and the medial rim of the squamosal body (Fig. 2.48). The same condition is indicated in BMNH 42745 (Fig. 2.55): the long supraoccipital shelf, the less diverging squamosal processes of the parietals, and the broad, almost parallel medial rims of the squamosal leave little room for a wide supratemporal fenestra. Similarly, the left and right descending surfaces of the squamosal processes of the parietals of SMNS 4059 reduce the width of the supratemporal fenestrae (Figs. 2.45, 2.46). An interpretation of the temporal condition of both specimens close to SMNS 12593 seems more likely than the presence of a broad supraoccipital shelf, the more diverging parieto-squamosal bar, and the steeply descending squamosal processes of *Nicrosaurus kapffi*. However, the incomplete preservation and the deformation (especially SMNS 4059) in these specimens prevent a full corroboration.

Quadratojugal and jugal. The specimens with well preserved lateral skull profile (SMNS 12593, BMNH 42745) show a very pronounced flaring of the ventral part of the cheek resulting in a longitudinal depression of the quadratojugal which extends also onto the jugal (Figs. 2.47, 2.53, 2.55). The same character was already noted in some specimens of *Nicrosaurus kapffi*, but is never developed to such a degree in this taxon. For this reason, the whole cheek region of *Nicrosaurus* species B is mediolaterally thin and delicate. Likewise, the jugal-quadratojugal bar is remarkably thin and sharp-edged in ventral view (Figs. 2.46, 2.49, 2.56), whereas in the majority of *Nicrosaurus kapffi* the same edge is comparatively thick and always rounded. A fracture on the left side of BMNH 42745 demonstrates that the jugal is inserted into the quadratojugal in the way described for *Nicrosaurus kapffi*.

Quadrate. In contrast to Nicrosaurus kapffi, the posteroventral rim of the quadrate including the articulation surface with the mandible is strongly extended posteriorly. This leads to a deeply concave posterior outline of the bone in lateral view and contributes to the broad appearance of the tympanic fossa (SMNS 12593: Fig. 2.53). The craniomandibular joint surface of the quadrate is less massively developed and rather narrow transversely. In *Nicrosaurus* species B, the lateral condyle is offset from the

cheek as well (BMNH 42745), the step between condyle and quadratojugal reaching a figure of 50 mm in SMNS 4059.

Ventral aspect and palatal complex

Premaxilla. The alveolar ridges are incipiently flatter, while being of similar width to these of *Nicrosaurus kapffi*. However, because of the narrow and delicate snout, the ridges appear more conspicuous and are well distinguished from the alveoli also in the posterior part of snout (e.g. BMNH 42745: Fig. 2.56). The alveolar ridges are commonly visible in lateral view, depending on the degree of compaction, and the alveoli are set more dorsally than in *Nicrosaurus kapffi*, and are thus visible in lateral view as well (BMNH 42745: Fig. 2.57, SMNS uncat. no. 11: Fig. 2.63).

Maxilla. A ridge in the extension of the palatine-maxilla suture leading to the maxilla-premaxilla contact might suggest that the maxilla is excluded from the choana (SMNS 4059: Fig. 2.46, SMNS 12593: Fig. 2.50A, GPIT 2070.001, right-hand side: Fig. 2.61). In the last two mentioned specimens, the actual sutures are better preserved than in the SMNS 12593 and a choanal contact of the maxilla can be established for *Nicrosaurus* species B. A ridge in the same position is present also in the narrow-snouted *Nicrosaurus kapffi* BMNH 42743, and since all these specimens show evidence of crushing in the narial region, the ridge may represent a fracture along a zone of weakness on the palate as a result of dorsolateral compression.

Vomer. Much variation can be seen in the shape and morphology of the vomers. Anteriorly, the bones form a slender, tapering prong, which is usually not laterally expanded to a rhombic shape as in *Nicrosaurus kapffi* - with the exception of GPIT 2070.001 (Fig. 2.61). The vomers are clearly separated over their whole length (BMNH 42745: Fig. 2.56, GPIT 2070.001: Fig. 2.61), whereas no suture is visible in SMNS 4059 (Fig. 2.46) and SMNS 12593 (Fig. 2.50A). The prechoanal part may be trough-like (SMNS 12593: Fig. 2.49) in contrast to the vaulted vomers in GPIT 2070.001, which are confluent with the interpremaxillary suture on a low ridge in this specimen (Fig. 2.61). The interchoanal septum starts as a rounded ridge becoming a sharp and steep V-shaped structure posteriorly (GPIT 2070.001: Fig. 2.61, SMNS 12593: Fig. 2.50B). The vomers terminate in a transverse suture behind the choanae.

Palatine. The morphology of the palatine and the palatal ridge is described based on SMNS 12593 and illustrated in Figure 2.50. At the anterior border of the choana, the palatine is shaped as a rounded broad palatal ridge that forms a vertical wall bordering the

choana. More posteriorly, the ridge becomes sharp-edged and the slope of the choanal border is oriented 75° upward and outward. Gradually, the palatal ridge decreases in height and runs laterally in a gentle curve. The palatal ridge now separates a gently rounded medial part of the palatine that spans one third of the bone width and slopes toward the palatal vault from the horizontal to slightly dorsolaterally sloping remaining two-thirds of the palatine. At the medial edge of the palatine, a more dorsally placed ridge appears, resulting in an angular, increasingly more deflected lateral wall of the choana. From the level of the posterior third of the choana posteriorly, this ridge is developed into a sharp-edged horizontal flange overhanging the choana and subsequently the palatal vault. The flange lies approximately 5 mm above the level of the palatal ridge. BMNH 42745 is the only specimen in which the sutures on the palatal vault are comparatively well preserved. As in *Nicrosaurus kapffi*, the palatine extends onto the roof of the palatal vault and meets its counterpart at the mid-line behind the vomers (Fig. 2.56).

Suborbital fenestra. The suborbital fenestra is slender, slit-like and somewhat constricted in its middle part as in *Nicrosaurus kapffi* (SMNS 4059, left-hand side: Fig. 2.46). In SMNS 12593, the suborbital fenestra continues posteriorly as a deep groove onto the pterygoid flange, which distinguishes the palatine-pterygoid complex from the ectopterygoid (Fig. 2.49). The groove is approximately in the same position as the ectopterygoid canal or ectopterygoid depression described in other phytosaurs (CAMP 1930; CASE 1929; DOYLE & SUES 1995), and could represent a homologous structure, especially since the pterygoid flange is damaged here, and the groove could actually represent a ventrally open canal. A similar groove, or evidence for a canal, is not, or only rudimentarily, expressed on the pterygoid flange of SMNS 4059, and in all specimens of *Nicrosaurus kapffi*.

Palatal vault and pterygoid. The depth of the palatal vault is similarly variable as in *Nicrosaurus kapffi* (Tab. 2.3.1). At the posterior end of the choana, the palatine forms a plane sloping medially at c. 45° into the opening, which slowly turns into a vertical orientation anteriorly (Fig. 2.49). The interpterygoid suture is especially well developed as a groove in BMNH 42745 (Fig. 2.56) and in the posterior part also in SMNS 4059 (Fig. 2.46).

Ectopterygoid. A large foramen is situated in the anteroventral corner of the infratemporal fenestra at the suture of the ectopterygoid with the jugal (SMNS 4059: Fig. 2.46, SMNS 12593). The ectopterygoid shows also a well developed ascending process along the postorbital process of the jugal (Fig. 2.46).

Pterygo-quadrate plate. The pterygo-quadrate plate shows the same orientation as in *Nicrosaurus* kapffi and is similarly deflected into a horizontal position, but the bar is markedly thinner and comparatively wider in *Nicrosaurus kapffi*, and lacks the opposing grooves on the ventral surface (SMNS 12593: Figs. 2.49, 2.54). The height of the quadrate wing of the pterygoid diminishes rapidly towards the base and the process ends in a sulcus floored by the pterygo-quadrate bar and a thick and prominent, but short, ridge along the pteroccipital fenestra (Fig. 2.54). This ridge is not present in *Nicrosaurus kapffi* (e.g. BMNH 42743: Fig. 2.25). The dorsal process of the quadrate wing is long and slender. Although its extremity is obliterated by damage, the traces on the surface of the quadrate show that the process almost touches the paroccipital process of the opisthotic (BMNH 42745: Fig. 2.56).

Occipital aspect and braincase

Supraoccipital. The supraoccipital shelf is elongated anteroposteriorly and narrower because of the less diverging squamosal processes of the parietals, rather than the hemicircular outline in *Nicrosaurus kapffi*. The elongation is especially obvious in the posterior part of the shelf which is deflected into an almost horizontal plane (BMNH 42745: Fig. 2.55, SMNS 12593: Figs. 2.48, 2.54), and for this reason its posterior edge is more prominent. The supraoccipital extends considerably to the side and clearly participates in the border of the posttemporal fenestra for a considerable distance dorsomedially (BMNH 42745: Fig. 2.59).The supraoccipital reaches downward over the whole length of the posterior edge of the supraoccipital shelf. The bone then narrows to a tongue which forms the centre of the roof of the foramen magnum (SMNS 12593: Fig. 2.54, BMNH 42745: Fig. 2.59).

Posttemporal fenestra. The posttemporal fenestra is similarly located as in *Nicrosaurus kapffi* over the medial half of the paroccipital process (BMNH 42745: Fig. 2.59, SMNS 12593). In SMNS 12593, it is more elongated, reaching beyond the midpoint of the paroccipital process (Fig. 2.54). For this reason, and mainly caused by the more delicate occipital structures of *Nicrosaurus* species B, it appears to be larger. In actual figures, the size of the posttemporal fenestra of *Nicrosaurus* species B falls within the size range exhibited by *Nicrosaurus kapffi* (Tab. 2.3.1).

Exoccipital. The exoccipitals meet in front of the condyle and form the complete floor of the foramen magnum (BMNH 42745: Fig. 2.59, SMNS 12593). In both specimens, the exoccipitals are separated dorsally by the supraoccipital. Two horseshoe-shaped, dorsolaterally compressed scars are situated symmetrically on the exoccipitals at

the fringe of the supraoccipital shelf above the foramen magnum (Figs. 2.48, 2.54, 2.59). These might represent the facets for a proatlas (or rather the insertion of ligaments related to that element), which have been also mentioned for "*Parasuchus*" (CHATTERJEE 1978).

Opisthotic. The medial part of the paroccipital process is dorsoventrally flattened. A cross-section here would result in an elliptical outline with a sagitally directed long axis, which results in a more rounded ridge on the posterior face (BMNH 42745: Fig. 2.58, SMNS 12593: Fig. 2.51), in contrast to the stout shape and sharper posterior ridge in *Nicrosaurus kapffi*. The dorsoventral expansion of the paroccipital process is achieved entirely by means of a well distinguished ventral opisthotic ridge. In SMNS 12593, the paroccipital process is laterally strongly compressed in anteroposterior direction (8 mm at maximum decreasing to 4.5 mm at the extremity), resulting in more space for a comparatively broader tympanic recess (Fig. 2.49). The ventral opisthotic ridge occupies the whole ventrolateral aspect of the process, while in *Nicrosaurus kapffi*, there is a shelf left on the ventral surface of the paroccipital process just in front of the opisthotic ridge. For the same reason, the medial part of the paroccipital process is relatively broader than in *Nicrosaurus kapffi* (actual figure in SMNS 12593: 18 mm) and the whole process seems to be elongated and slender in occipital view (Fig. 2.54). The posterolateral surface of the paroccipital process is more convex than in *Nicrosaurus kapffi*. There is no evidence for a lamella of the squamosal extending onto the paroccipital process (Figs. 2.54, 2.59).

The opisthotic lamella and the lateral wall of the stapedial groove are generally more prominent than in *Nicrosaurus kapffi*. A characteristic feature of the specimens of "*Belodon plieningeri*" is the much thicker opisthotic lamella with a broadly rounded ventral edge (BMNH 42745: Fig. 2.58, SMNS 12593: Fig. 2.51), in contrast to the sharp and slender lamella in *Nicrosaurus kapffi*. The medial flank of the opisthotic lamella slopes gently toward the exoccipital in ventral view, forming the floor of the broader and distally expanding jugular groove (SMNS 12593: Fig. 2.51). The jugular foramen is fully exposed in BMNH 42745. A constriction subdivides the jugular foramen into a large anterior opening and a vertical slit situated posteriorly, but both openings are still confluent. The single foramen nervi hypoglossi (XII) is incorporated in the recess of the jugular foramen (Fig. 2.58). Likewise, there is no indication of a foramen nervi hypoglossi penetrating the lateral face of the exoccipital pillar of SMNS 12593. The parallel-rimmed stapedial groove is the narrower of both grooves. In its proximal part, the stapedial groove of SMNS 12593 is bottlenecked by a prong of its lateral wall, which perhaps served to hold the stapedial footplate in position (Fig. 2.51).

Basisphenoid. The basal tubera face posteroventrally or even more to the posterior side (BMNH 42745, SMNS 12593). The transverse line seen on the posterior base of the tubera in SMNS 12593 (Fig. 2.51) represents a fracture. The tubera are close together and confluent in SMNS 12593, whereas in BMNH 43745 (and all specimens of *Nicrosaurus kapffi*) each tuber represents a separate entity divided by a longitudinal groove. A transverse ridge bridges the groove (Figs. 2.56, 2.58). In SMNS 12593, the tubera are expanded laterally and compressed anteroposteriorly. For this reason, the area between the tubera and the basipterygoid processes is markedly constricted (Fig. 2.49). The basioccipital contributes less to their ventral tuberal surface than in *Nicrosaurus kapffi* (c. 25% of total area), reaching the anterior rim of the tubera only by means of a median prong (Figs. 2.49, 2.55, 2.56). *Nicrosaurus* species B shows the same variation regarding the basisphenoid fontanelle as *Nicrosaurus kapffi*. The basisphenoid of SMNS 12593 (Fig. 2.49) shows a faint, but clearly developed fontanelle which trends from the anterior face of the tubera anteriorly along the midline. It finally leads into an oval foramen close to the anterior rim of the basisphenoid between the pterygoid processes, of which there is no hint in *Nicrosaurus kapffi*. Posteriorly, the fontanelle can be traced on the tuberal surface of the basioccipital as well. This contrasts with BMNH 42745, in which the basisphenoid is completely fused without any trace of a synchondrosis. The pterygoid processes of the basisphenoid are longer and less stout than in *Nicrosaurus kapffi* (SMNS 12593, BMNH 42745). The trough formed between the descending pterygoid processes is narrow and much deeper than in *Nicrosaurus kapffi*. On the flanks of the trough, the articular flange of each pterygoid process is separated from the stout base of the process by a sharp ridge which trails anteriorly, gently medially, and strongly dorsally. The ridge is unlikely to represent a fracture, since ridges occur symmetrically on both sides of the braincase of SMNS 12392, and the lateral and ventrolateral faces of the processes are otherwise intact.

Pteroccipital fenestra. As a result of the constricted basisphenoid corpus, the anterior part of the pteroccipital fenestra is medially expanded to a triangular shape. The wide base of the paroccipital process causes the posterior part of the fenestra to narrow to a mere slit (SMNS 12593: Figs. 2.49, 2.51).This is not the case to such a degree in BMNH 42745, and might be dependent on skull height.

Mandible

The two mandibles referred to *Nicrosaurus* species B have been described and figured by MEYER (1865b: pl. 23) and HUENE (1911: fig. 11), and since no further anatomical information can be provided it is unnecessary to duplicate their descriptions.

The anatomy resembles in great detail the mandible of *Nicrosaurus kapffi*, apart from the size disparity and the characters that are coupled with the dentition. The only remarkable differences between both species that cannot be attributed to allometry, and are therefore interpreted as distinguishing characters here, are the proportionally longer symphyseal length (Tab. 2.3.2), and the much lower width of the glenoid facet of *Nicrosaurus* species B.

Dentition

The upper dentition of *Nicrosaurus* species B is poorly known, being essentially represented by a row of four posterior out of 17 left maxillary teeth, m (11) to m (14), preserved *in-situ* in SMNS 4059 (Fig. 2.46). There are a number of poorly preserved and incomplete teeth scattered along the jaws of GPIT 2070.001, which provide few information.

Nothing is known about the morphology of the fangs, and the premaxillary dentition. The last alveoli in the premaxilla of *Nicrosaurus* species B are not enlarged, and all specimens lack the characteristic implantation of posterior premaxilla teeth of *Nicrosaurus kapffi*. The first maxillary alveoli are somewhat smaller compared to the preceding premaxillary sockets (BMNH 42745: Fig. 2.56; on the right side, also the last premaxillary alveolus; SMNS uncat. no. 11: Fig. 2.63). Additionally, several specimens show a weak second constriction of the snout at the joint of premaxilla and maxilla (e.g. BMNH 42745: Fig. 2.56, GPIT 2070.001: Fig. 2.60).SMNS 4059, which lacks a corresponding constriction, nevertheless shows three smaller and more closely spaced alveoli (Fig. 2.46). They are interpreted as the first three maxillary alveoli here, although the premaxilla-maxilla suture is not preserved in the specimen. The second constriction and size reduction of the first maxillary alveoli could be interpreted as the start of a maxilla set, and consequently the dentition of *Nicrosaurus* species B might be considered facultatively tripartite like *Nicrosaurus kappfi*. However, it must be considered that in *Nicrosaurus* species B the size disparity of the alveoli at the border of premaxilla and maxilla is insignificant compared to *Nicrosaurus kapffi*, and that dental sets are defined by a suite of morphological transformations along the jaw, of which size is only one criterion. As long as there is no evidence for morphologic disparity between posterior premaxillary and anterior maxillary teeth, I regard it as more likely that the upper dentition of *Nicrosaurus* species B is bipartite with a tip-of-snout set, and one post-tip set comprising all upper teeth except the anteriormost four.

The maxillary teeth are best characterised by comparison with teeth of *Nicrosaurus kapffi* in similar positions, and I refer to MEYER (1865b: pl. 29 fig. 5) for illustrations of

these teeth. The maximum tooth crown height is 11 mm, which represents about half the height of similar teeth in *Nicrosaurus kapffi*. Fore-aft basal length ranges from 7 - 8 mm, and basal width is 5 mm. In labial view, the teeth are thus much taller as expressed by the ratio tooth crown height to fore-aft basal length of 1.6, in contrast to 1.07 in m (15) and m (17) of *Nicrosaurus kapffi*. The basal dimensions are more similar in both species, fore-aft basal length to basal width is 1.4 in *Nicrosaurus* species B and m (15) in *Nicrosaurus kapffi*, rising to 1.7 in m (17) of the latter. As common in posterior maxillary teeth of phytosaurs, the crown is bicarinate and finely serrated. The maxillary teeth bear much less well developed flanges than in *Nicrosaurus kapffi*, although the teeth are similarly mesiodistally asymmetric with flanges clearly demarcated from the body of the crown. Consequently, posterior maxillary teeth of *Nicrosaurus* species B show only a slight trace of a basal constriction. The labial side is vaulted, showing in comparison to *Nicrosaurus kapffi* a more prominent central spine that runs from the apex towards the base and faints at about mid-height of the tooth crown. The apices of the maxillary teeth are not, or only insignificantly, recurved and thus lack the distally overhanging tips seen in *Nicrosaurus kapffi*.

The mandibular tooth morphology is better documented than the upper dentition by the almost complete dentition of BMNH 38038 (MEYER 1865b: pl. 23 fig. 2), with additional information from well preserved anterior mandible teeth in GPIT 261/011.

Tooth crown heights are constant along the entire mandibular ramus showing about 9 mm for fully erupted teeth. In the anterior section of the dentary behind the rosette, the teeth are conical with straight tooth axes. The basal half of the tooth crown is round in cross-section with a diameter of maximal 3.5 mm, which diminishes only little further upward. In the apical half, the crown tapers rapidly and ends in an acute tip. There are no carina discernible, but in both specimens the teeth are still largely embedded in matrix which might obscure such details. The tooth crown shows an ornamentation of fine vertical furrows that separate broader, blunt ridges and fade at about mid-height of the crown. The apical half of the crown is unsculptured.

Only about the last dozen dentary teeth are specialised and resemble broadly their counterparts in the posterior section of the maxilla in being lingually flattened, bicarinate, and serrated. The maximum fore-aft basal length is 7 mm. However, in contrast to maxillary teeth, the labial side is less vaulted and the central spine present on the labial side of the crown continues over the whole crown and is even drawn out apically. This results in a peculiar knob-shaped tip. The fully serrated carinae are not extended onto the apical knob.

2.3.4 Character discussion

2.3.4.1 The status and generic referral of "*Belodon plieningeri*"

No previous author demonstrated derived autapomorphic states shared by the specimens referred here to *Nicrosaurus* species B. Until now, "*Belodon plieningeri*" sensu MEYER (1861) has always been characterised by features which are plesiomorphic within *Nicrosaurus*; most commonly, the taxon has been distinguished by the primitive traits of the diagnostic characters of *Nicrosaurus kapffi*. LONG & MURRY (1995: 62) included the taxon among their Pseudopalatinae and remarked that the specimens "closely resemble *Pseudopalatus*, although they appear to be less derived", but failed to substantiate their claim by any derived (relative to *Nicrosaurus kapffi*) or less derived (relative to *Pseudopalatus*) character. The redescription identified six characters of the "*Belodon plieningeri*"-assemblage, most of them represented in the temporal region of SMNS 12593, which are unequivocally derived in relation to *Nicrosaurus kapffi*: a reduced height of the postorbito-squamosal bar, an angular rim of the squamosal, a raised external narial opening, an elongated squamosal, a pointed posterior tip of the squamosal, and reduced width of the supratemporal opening. However, a variety of problems are related with these characters. Most importantly, the distribution among the specimens referred to "*Belodon plieningeri*" is uninformative or not present in all specimens, and of similar character states are present in other, perhaps closely related phytosaur taxa. This render an assignment of these characters difficult for "*Belodon plieningeri*". These characters may have the potential to be valid autapomorphies and could argue for the monophyly of the assemblage, but similarly for a closer relationship of one or more specimens with *Pseudopalatus* and *Arribasuchus*. The subject of this section is to discuss the evidence and find a solution for these problems.

(1) height of the postorbito-squamosal bar

In "*Belodon plieningeri*", the height of the postorbito-squamosal bar (Tab. 2.3.1), taken at its maximum amount at the anterior corner of the supratemporal fenestra, is approximately half as great as in *Nicrosaurus* kapffi (Tab. 2.2.1). The character state is apparently constant in both the high-domed and low-domed morph of "*Belodon plieningeri*", and discrete values are available to distinguish it from the other species. The character state seems also not to be linked with the lesser robustness of the skull of the specimens, because even the most gracile *Nicrosaurus kapffi* BMNH 42743 shows a value of 18 mm.

Doubts about the distinction emerge when incomplete specimens are taken into account. The isolated squamosal BMNH 38043, which is in every feature similar to *Nicrosaurus kapffi*, has a maximum thickness of only 13.4 mm. However, the specimen lacks the anterior part of the postorbito-squamosal bar, and the value could approach the typical amount if taken at the same spot as in the complete *Nicrosaurus kapffi* skulls. The more problematic specimen is BMNH 38042, an isolated left postorbito-squamosal bar that can only be identified as *Nicrosaurus* sp., but shows closer affinities to "*Belodon plieningeri*" in having a higher squamosal with a tapering tip. In this specimen, the thickness of the bar at the anterior corner of the supratemporal fenestra is 15.2 mm, and the specimen thus exactly bridges the gap between "*Belodon plieningeri*" and *Nicrosaurus kapffi*.

Another problematic aspect is the polarity and distribution of the character within Phytosauria. I was unable to locate precise descriptions or measurements of the relative or absolute thickness of the postorbito-squamosal bar in phytosaur taxa on the basis of the current literature. Cross-sections of the bar in *Smilosuchus* (CAMP 1930: figs. 29, 30, 37) suggest a primitively thick condition. *Smilosuchus* and *Leptosuchus*, however, show a much more reduced width of the bar and the horizontal plane of the squamosal compared to *Nicrosaurus*, and this condition is likely to have influenced positively the thickness of the postorbito-squamosal bar for stability reasons. On the other hand, this observation is in conflict with the statement that *Nicrosaurus*, *Pseudopalatus*, *Arribasuchus*, and *Mystriosuchus* can be united by the synapomorphy "postorbital bar is [...] thicker and shorter than in other groups" (BALLEW 1989: 326, character 34). No ingroup comparisons are presented regarding the character in question, and this is almost impossible to undertake without examining the actual specimens. The character is also easily confused with her character 12b, "squamosal has become compressed", which actually refers to the posterior process only. BALLEW's description is certainly correct for *Mystriosuchus*, which shows an enormously thickened postorbito-squamosal bar (see subsection 3.3.2), again correlated with a comparatively lesser width of the postorbito-squamosal bar in dorsal view.

The monophyletic state of the clade *Nicrosaurus* + *Arribasuchus* + *Pseudopalatus* + *Mystriosuchus* is supported by more characters than the thickness of the postorbito-squamosal bar (see BALLEW 1989; chapter 5). Pending a revision of the character distribution, I accept BALLEW's character description and suggest that the reduced thickness of the postorbito-squamosal bar of "*Belodon plieningeri*" is a derived character state within the clade. There are still doubts left about the character state discrimination, but the state seen in SMNS 12593, BMNH 42745, and GPIT 2070.001 (9-13 mm) has

at the moment the greatest potential of all characters discussed here to represent a valid autapomorphy of "*Belodon plieningeri*".

(2) medial rim of squamosal angular

The morphology of the squamosal tip is naturally an expression of the shape of the dorsal surface of the bone. All specimens of "*Belodon plieningeri*" possess the characteristically short and broad postorbito-squamosal bar of *Nicrosaurus*, *Pseudopalatus* and *Arribasuchus*. In SMNS 12593, the posteromedial rim of the squamosal is set at an angle to the medial rim of the postorbito-squamosal bar (Fig. 2.49). This finally results in the distinctly pointed squamosal of the specimen. *Nicrosaurus kapffi* shows an anteroposteriorly directed rim, or a dorsal surface of the squamosal which is straight, but slightly diverging. An angular medial rim of the squamosal is not present in *Pseudopalatus*, *Arribasuchus*, and *Mystriosuchus*, and is thus a possible autapomorphic state. The angle of the posterior process of "*Belodon plieningeri*", however, is found in one *Nicrosaurus kapffi*, SMNS 5727, although the specimen still shows a rounded tip of the squamosal much more similar to the broadly rounded posterior process in the other specimens (see part 2.2.5.2). This specimen therefore represents an intermediate stage regarding this character, an angular medial rim of the posterior process combined with a rounded tip, rendering a character definition difficult. For this reason, the character seems unsuitable for clear taxonomic and probably phylogenetic usage. Both character states found in *Nicrosaurus*, however, differ from the shape of the medial squamosal rim in *Pseudopalatus* and *Arribasuchus*, in which the dorsal surface of the squamosal including the posterior process is more derived in tapering continually towards the tip, and in some extreme conditions has been described as "stiletto-like" (LONG & MURRY 1995: 48).

A metataxon like "*Belodon plieningeri*" in the current definition can, but need not necessarily, represent a paraphyletic assemblage of specimens. Three temporal characters of SMNS 12593 and one feature of the naris in GPIT 2070.001 show developments which are interpreted as apomorphic in relation to other specimens of the genus *Nicrosaurus*. Indeed, these character states occur at least in one clearly more derived phytosaur taxon, *Pseudopalatus*.

(3) raised narial rims

The crater-like nares of GPIT 2070,000 with prominently raised narial rims that are well demarcated from the prenarial snout and the orbitonasal region (Fig. 2.62) represents a character state not developed in *Nicrosaurus kapffi*, but also lacking among

the other specimens of "*Belodon plieningeri*". However, it is principally present also in *Pseudopalatus pristinus* and *Arribasuchus buceros*. The nares of the type of *Pseudopalatus* have been characterised as being "situated on a distinct prominence that is accentuated by its rather abrupt rise from the rostrum in front, and a saddle-shaped depression behind" (MEHL 1928b: 9), and the description is corroborated for additional specimens by BALLEW (1989) and LONG & MURRY (1995). Similarly, a number of specimens now referred to *Arribasuchus buceros* (e.g. MEHL 1922) show a demarcated narial crater, but the structure is not as conspicuous as in *Pseudopalatus* because of the presence of a prenarial crest. BALLEW (1989) noted that a sloping posterior narial border occurs in other taxa as well (quoting *Leptosuchus adamanensis* and *Angistorhinus talainti*), but a "convexity of the nasals forming a complete rounded rim" (p. 329) is said to be unique to *Pseudopalatus pristinus*, and thus possibly autapomorphic (BALLEW 1989: character 58). I have some difficulties understanding the character state as formulated. Does it mean "crater-like" only, i.e. the narial rim is distinctly raised relative to the surrounding? Is the "complete rounded rim" to be taken literally in the meaning of being on the same level without interruption by an anterior groove or what is termed here the narial wing, or is it merely an illustrative addendum in imitation of CAMP's (1930) distinction between circular or compressed shape of the naris? *Mystriosuchus planirostris* has a very prominent and cone-like nasal opening, in which the tip of the nares continues in a large gap of the narial rim anteriorly, and therefore is not completely surrounded by a levelled rim. BALLEW's explicit restriction of the character to *Pseudopalatus pristinus* indicates that the second interpretation is meant. However, the very same condition as in *Mystriosuchus* pertains to the holotype of *Pseudopalatus pristinus* (MEHL 1928b: 9; LONG & MURRY 1995: fig. 40B), thus clashing with BALLEW's "complete rim". Both *Mystriosuchus* and the type of *Pseudopalatus* contrast with GPIT 2070.001, in which the distinctly raised narial rim encompasses the whole nasal opening without a narial wing and an anterior narial groove (Fig. 2.60). The latter condition additionally occurs among specimens referred to *Rutiodon carolinensis* (COLBERT 1947; GREGORY 1962b: fig. 6). Hence, also the character state "fully elevated narial rim" or "crater-like nares" is found in a variety of genera, which hardly form a natural clade.

In conclusion, there are two different character states developed in the narial region of phytosaurs: the "crater-like" shape, i.e. the narial rim is distinctly raised relative to the pre- and postnarial area, and, secondly, the nares are completely surrounded by a wall-like narial rim. The character distribution are so randomly distributed among phytosaur taxa, that neither the crater-like nasal shape nor the complete narial rim without anterior narial groove seems to be a taxonomically useful character. The presence of crater-like rims in GPIT 2070.001 does not justify separation of the specimen from the "*Belodon plieningeri*"-assemblage.

Another aspect of the nares has to be discussed in this context. In contrast to the majority of specimens of *Pseudopalatus* and *Arribasuchus*, the elevation of the nasal openings in GPIT 2070.001 is not that prominent and remains distinctly below the level of the skull table, the posterior rim being approximately level with the interorbital depression. According to BALLEW (1989: character 40), the narial opening raised above the skull roof constitutes the decisive synapomorphy of the two North American taxa, plus *Mystriosuchus*, the character state according her analysis being reversed in this genus. LONG & MURRY (1995) established the clade Pseudopalatinae comprising *Pseudopalatus*, *Arribasuchus*, and *Nicrosaurus*. The vertical position of the naris is not explicitly listed as an autapomorphy, but according to the discussion (LONG & MURRY 1995: 49, 57) it is the most important character to distinguish the North American pseudopalatine phytosaurs from the less derived European taxa.

A number of problems arise when this character is closely examined. Most importantly, there are inconsistencies regarding the relative height of the nares among the specimens referred to the same species, and consequently among the genera constituting the clade *Pseudopalatus* + *Arribasuchus*. In contrast to at least some of the referred specimens (e.g. BALLEW 1989: pl. 6 fig. C), the holotype of *Pseudopalatus pristinus* does not show nares which are positioned at a higher level than the skull table (MEHL 1928b: pl. 1 fig. C; LONG & MURRY fig. 41A). The same is the case in the holotype of *Arribasuchus buceros*, in which the nares are evidently placed below the level of the skull roof (HUENE 1915a; HUNT 1993b). The "depressed" nasal openings of the type of *Arribasuchus buceros* have been attributed to preservational circumstances like crushing (LONG & MURRY 1995), but according to the illustrations available, it is doubtful whether the same explanation can be applied to the type of *Pseudopalatus pristinus* as well. It is important to note that the presence of this character has to be challenged in the type specimens of both species. This leaves two possibilities. Perhaps both character states occur within a species. It follows that the threshold between the plesiomorphic and apomorphic character state (below or above skull level) is purely arbitrary, based on the observation that some specimens show an apparently well definable derived character state, which in fact represents the extreme in a gradual variation at the species level. Hence, the character cannot be safely utilised in establishing phylogenetic hypotheses. Alternatively, if the distinction between both character states and the phylogenetic interpretation is deemed real and is to be rigorously maintained, the incongruent distribution must have severe consequences for the specific, and since both taxa represent the type species, also the generic diagnosis and the composition of the taxa. This has been exercised for "*Belodon*" *buceros* by HUNT (1993b) and HUNT & LUCAS (1993a,b), who transferred the species from *Pseudopalatus* (*sensu* BALLEW 1989) to *Nicrosaurus* because the type specimen lacks the autapomorphic strongly elevated nares. Neverthe-

less, *Pseudopalatus pristinus*, *Arribasuchus buceros*, and the clade *Pseudopalatus* + *Arribasuchus* + *Mystriosuchus* is still supported by other synapomorphies (BALLEW 1989; chapter 5), and these need to be carefully discussed elsewhere. I do not wish to decide on the matter until I have the opportunity to examine the specimens in question.

Several authors emphasise that the nasals in some of the specimens which show strongly elevated narial openings are thickened and have roughened narial rims and internarial septa (*Arribasuchus buceros*: CAMP 1930: 52; *Pseudopalatus pristinus*: BALLEW 1989: 329). It remains to be determined whether this condition can be considered normal or represents a pathologically altered bone surface, which could be responsible for the extraordinary elevation of the narial rim.

In summary, there are considerable doubts whether the character "elevation of narial rims" has real taxonomic (and phylogenetic) significance, as suggested by the majority of workers. The crater-like nasal openings elevated above the skull roof are also present in *Angistorhinus alticephalus* (MURRY 1989; LUCAS *et al.* 1993) and approach this condition closely in *Angistorhinus talainti* (DUTUIT 1977a: pl. 1 figs. A,B; pl. 2 fig. D). Thus the elevation apparently arose independently within the genus *Angistorhinus* as well.

(4) squamosal body elongated

Both specimens SMNS 12593 and BMNH 42745, in which the body of the squamosal is completely preserved, demonstrate that the body of the squamosal is longer than in *Nicrosaurus kapffi*. It is difficult to express the character state in quantitative terms, i.e. by measurements or indices. It may be defined as follows: the anterior rim of the paroccipital process of the squamosal is situated behind the level of the extremity of the quadrate. Another consequence of the elongated squamosal body is that the opisthotic, braced against the paroccipital process of the squamosal, projects further backward. It is probably more appropriate to fix the character state using a corollary feature. The tympanic fossa is wider in lateral view, and SMNS 12593 shows the roof of the fossa not shaped as a cleft like *Nicrosaurus kapffi*, but in a broadly rounded arc. However, the rounded roof seems to have been absent in BMNH 42745. The roof of the tympanic fossa has unfortunately been damaged after MEYER (1865b) drew the specimen, and it is impossible to check the accuracy of the figure given. Furthermore, our knowledge of the intraspecific variation in the width of the tympanic fossa in other taxa is poor, and figured specimens of *Leptosuchus* (CAMP 1930; BALLEW 1989; LONG & MURRY 1995) show this feature to be inconsistent.

It is evident that in *Pseudopalatus* and *Arribasuchus* the squamosal body is elongated anteroposteriorly as well, and this character state represents a derived condition. Likewise, in both taxa the tympanic fossa is rounded in lateral view (MEHL

1922: fig. 1, 1928b: pl. 1 fig. C; LONG & MURRY 1995: fig. 41C). In contrast to the evidence from SMNS 12593, both genera show an elongated and far more posteriorly projecting posterior process of the squamosal (HUENE 1915a; BALLEW 1989; LONG & MURRY 1995).

(5) pointed posterior process of squamosal

The posterior process of the squamosal of SMNS 12593 terminates in a pointed tip (Fig. 2.47), in contrast to the broadly rounded tip in *Nicrosaurus kapffi*. The polarity of the character within Phytosauridae is not obvious, because the successive outgroups (*Leptosuchus*, *Smilosuchus*, and Angistorhininae) include both forms with pointed and rounded squamosal tips (subsection 5.3.2, (32)). According to more derived phytosaurs, a pointed tip of the squamosal is the derived character state (BALLEW 1989). I am, however, reluctant to propose this character state as an autapomorphy of "*Belodon plieningeri*", for two reasons. Firstly, I wish to point out that actually only in two specimens, the SMNS 12593 and BMNH 38037, is the posterior process of the squamosal completely preserved and shows this character state. BMNH 38037, as discussed below, is specifically indeterminable and even cannot be excluded from *Nicrosaurus kapffi* because of the missing rostrum. Note also, that in the gracile morph of *Nicrosaurus kapffi* the tip of the squamosal is unknown and therefore it is by no means excluded that the shape of the squamosal tip is dimorphic in this species. Thus there is no evidence that SMNS 12593 is representative of the whole "non-*kapffi*" *Nicrosaurus* assemblage. Moreover, if "*Belodon plieningeri*" were to be defined by this character state, in a strict sense only SMNS 12593 could be included in that taxon, and this would leave effectively all other specimens of *Nicrosaurus*, which are not referable to *Nicrosaurus kapffi*, in a taxonomic limbo. Secondly, since a pointed squamosal tip also occurs in *Pseudopalatus* and *Arribasuchus* (BALLEW 1989; LONG & MURRY 1995), the feature may either characterise a more inclusive ingroup within Phytosauridae (consequently leaving the genus *Nicrosaurus* a paraphylum) or represent a homoplasy. As a matter of fact, regarding the character complex "squamosal" only, SMNS 12593 can only be segregated from *Pseudopalatus* and *Arribasuchus* by combining the character state "pointed posterior process" with more primitive features such as the shorter length of the process or the non constantly tapering shape in dorsal view. Homoplastic characters can be informative, but the very close relationship of *Nicrosaurus* to *Pseudopalatus* and *Arribasuchus* (BALLEW 1989; LONG & MURRY 1995) renders the validity questionable.

Finally, it must be noted that there are apparently also difficulties either with the definition of discrete character states or the distribution of the derived character state within species. The squamosals of some specimens of *Pseudopalatus pristinus* are clearly

in accord with the formulation of the derived state (e.g. LONG & MURRY 1995: fig. 40A). It needs some imagination, however, to recognise that the type of *Pseudopalatus pristinus* has a pointed squamosal (MEHL 1928b: pl. 1 fig. A; LONG & MURRY 1995: figs. 40B, 41B). As with the raised crater-like rim of the naris, the type of *Pseudopalatus pristinus* seems to be less derived than some members of the species it is representing. Similar differences in the pointedness of the extremity of the squamosal were reported by DOYLE & SUES (1995) in the *Rutiodon carolinensis* assemblage.

(6) width of supratemporal fenestra reduced

SMNS 12593 shows a considerably narrowed supratemporal fenestra compared to *Nicrosaurus kapffi*. The supratemporal fenestrae in SMNS 12593 can well be described as slit-like at least in their posterior sections (Fig. 2.48). The observation is at least in part supported by the two other specimens of "*Belodon plieningeri*", in which the supratemporal fenestra is partially preserved (BMNH 42745: Fig. 2.55, SMNS 4059). Note that in all specimens there is no distinction from *Nicrosaurus kapffi* in the anterior width of the supratemporal fenestra.

The gradual reduction of the supratemporal fenestra is a long-recognised, apomorphic trend among phytosaurs (CAMP 1930; GREGORY 1962b; BALLEW 1989; HUNT & LUCAS 1993c; LONG & MURRY 1995). It is most conspicuously expressed in the lineage of pseudopalatine phytosaurs (in the definition of LONG & MURRY 1995) from North America. *Pseudopalatus pristinus* shows overall narrow, slit-like supratemporal openings. In some extreme examples, included within the genera *Pseudopalatus* and *Arribasuchus* by LONG & MURRY (1995), the reduction can result in a virtual closure of the opening on the skull roof (HUNT & LUCAS 1993c). A similar trend is also evident, convergently, within the genus *Angistorhinus* (LONG & MURRY 1995), in which the wide opening of *Angistorhinus grandis* (MEHL 1913) is reduced to long, crescentic, slender slits in *Angistorhinus talainti* (DUTUIT 1977a).

Is it advisable to postulate an intermediate character state such as "posterior supratemporal fenestra slit-like"? This seems to makes sense regarding the final outcome, a reduction of the supratemporal fenestra to a slit, but neglects the different modes by which the derived character state is achieved. In *Pseudopalatus* and *Arribasuchus*, the supratemporal fenestra is transversely restricted over the whole length and finally almost closed by an increased medial expansion of the postorbito-squamosal bar (LONG & MURRY 1995). In this context, the vertical orientation of the squamosal processes of the parietals, resulting in the rounded parietal-supraoccipital complex, is a spatial prerequisite that allows the width of the squamosal to increase to bridge the supratemporal fenestra. SMNS 12593 retains the proportionally less broad parieto-squamosal bar of *Nicrosaurus*. The supratemporal fenestra is narrowed in its posterior part mainly by the gentle descent

of the squamosal process of the parietal, which thus approaches the medial rim of the squamosal. SMNS 12593 is even more primitive than *Nicrosaurus kapffi* regarding this character. The parietal-supraoccipital complex still retains its plesiomorphic angular outline. The reduction in SMNS 12593 also affects only the posterior part of the fenestra, which is still comparatively wide open in the type of *Pseudopalatus pristinus* (LONG & MURRY 1995: fig. 41B). The slit-like shape of the supratemporal fenestra in SMNS 12593, and probably "*Belodon plieningeri*", therefore actually takes place in a different area of the fenestra and is achieved in a different way than in *Pseudopalatus* and *Arribasuchus*. This suggests that the states of the supratemporal fenestra in *Nicrosaurus* and *Pseudopalatus* and *Arribasuchus* represent two superficially similar, but that arose independently. Furthermore, since the width of the supratemporal fenestra in SMNS 12593 is a result of the shallower slope of the dorsal rim of the squamosal process of the parietal, the character state is actually a plesiomorphic condition, and even uninformative regarding the relationship to *Nicrosaurus kapffi*.

Another problem turns up again among the pseudopalatine lineage: where to draw a line between gradually differing character states. The non-discrete nature of the width of the supratemporal fenestra is well reflected by the taxonomic assessment. HUNT & LUCAS (1993c), focusing on the extreme ends of the grade, erected the new genus *Redondasaurus* with two species for pseudopalatine specimens with almost closed supratemporal fenestrae in dorsal view. LONG & MURRY (1995) did not accept *Redondasaurus*, but recognised merely two genera in the Norian of the south-western United States, the gracile and slender-snouted *Pseudopalatus* and the robust, crested *Arribasuchus*. They put more weight on the gradual transition of the character, in their words on the grounds that "near to complete concealment of the supratemporal fenestra is typical of the southwestern pseudopalatines" (1995: 53-55).

Conclusions:

The observations can be summarised as follows:

(1) All specimens of "*Belodon plieningeri*" share with *Nicrosaurus kapffi* a well developed infranasal recess. Additionally, BMNH 42745 show the palatines meeting at the midline of the palatal vault, and in the same specimen the hypoglossal foramen is integrated into the recess of the foramen ovale. Both character states are apomorphic with respect to less derived phytosaurs (*Smilosuchus*, *Leptosuchus*); the first one is definitely and the second likely to be present in *Nicrosaurus kapffi* as well.

(2) Among the specimens of the assemblage, there are six characters which are derived relative to *Nicrosaurus kapffi* and potentially represent autapomorphies for

"*Belodon plieningeri*". However, only one, the reduced width of the postorbito-squamosal bar, is definitely shared by three members of the assemblage. Furthermore, there are a variety of problems with these characters, such as poorly definable character states, uninformative or unknown distribution within phytosaurs, and, most importantly, unproven representativeness for the whole group.

(3) Additionally, three of these derived characters expressed in specimen SMNS 12593, the elongated squamosal, the narrow supratemporal fenestra, and the pointed squamosal tip, are also present in the genus *Pseudopalatus*, or the development in SMNS 12593 approaches the character states seen in *Pseudopalatus*. However, only the first character is unproblematic.

(4) All specimens of the assemblage lack a number of derived features which are characteristic of *Pseudopalatus* and *Arribasuchus*. These include: steeply sloping prenarial part of the rostrum, nares raised above the skull roof (but see discussion above), rounded parietal-supraoccipital complex, elongated and continuously tapering posterior process of the squamosal, small posttemporal fenestra (with exception of *Arribasuchus mccauleyi*, BALLEW 1989).

Do *Nicrosaurus kapffi* and "*Belodon plieningeri*" represent a monophylum?

There are good reasons to consider a monophyletic origin of *Nicrosaurus kapffi* and the specimens described in this chapter. This view is supported by two synapomorphies, the infranasal recess and the palatines meeting each other on the palatal vault. A third synapomorphy, the location of the hypoglossal foramen, has yet to be confirmed. The alternative is to place the assemblage, or at least SMNS 12593, nearer to *Pseudopalatus*. Since the specimens in question lack several derived characters of *Pseudopalatus* + *Arribasuchus* + *Mystriosuchus* listed above, they would require a new generic name and would have to be placed in a sistergroup relationship with this clade, corresponding to node M in the phylogenetic hypothesis of BALLEW (1989: fig. 1). The discussion of the characters shows, that out of four superficially similar characters more derived relative to *Nicrosaurus kapffi*, only one character "elongated squamosal" passes a critical reevaluation. The other characters are problematical for various reasons, only the pointed squamosal and the elongated squamosal having the potential to be additional synapomorphies pending a reinvestigation of *Pseudopalatus*. Hence, it is more parsimonious to postulate a monophyletic group consisting of *Nicrosaurus kapffi* and "*Belodon plieningeri*", and consequently the specimens are referred to the genus *Nicrosaurus*. It follows, that the derived characters of SMNS 12593 and BMNH 42745 (elongated squamosal, pointed squamosal tip, posteriorly reduced supratemporal

fenestra) and GPIT 2070.001 (crater-like elevation of the narial rim) are considered to have arisen independently from *Pseudopalatus* + *Arribasuchus* + *Mystriosuchus* within *Nicrosaurus* and are regarded as homoplastic character states.

Is "*Belodon plieningeri*" a monophylum or a paraphyletic assemblage?

Because of its distribution among the assemblage, the thickness of the postorbito-squamosal bar was shown to be a character that can, in its limits, unite the specimens of "*Belodon plieningeri*" in a monophylum. As outlined in the character discussion above, it is SMNS 12593, which is evidently more derived than any specimen of *Nicrosaurus kapffi* in the characters, elongated squamosal, reduced supratemporal fenestra and pointed squamosal tip. It needs to be discussed, whether the anatomical data known so far justifies a segregation of SMNS 12593 from the remaining specimens of the "*Belodon plieningeri*" assemblage, and whether SMNS 12593 needs to be placed in a more derived species on its own. Using the criterion of parsimony, the decision seems to be obvious: three clearly apomorph characters argue for a segregation, only one, problematic in some aspects, for monophyly of the whole assemblage. However, it cannot be decided based on the available evidence, that the same character states do not apply to the other specimens of "*Belodon plieningeri*". It may well be that the advanced state of SMNS 12593 is merely an artefact of the poor preservation of the remaining "*Belodon plieningeri*". Thus, the three characters give only clear evidence that SMNS 12593 belongs to a distinct species from *Nicrosaurus kapffi*, but cannot prove distinctiveness for the remaining "*Belodon plieningeri*". A segregation of the specimen has also little heuristic value and would only transfer unsolved problems. There would be still no autapomorphy for the remaining specimens of "*Belodon plieningeri*", and these must then either be left unassigned (*Nicrosaurus* sp.) or assembled in a metataxon. Moreover, I estimate the likelihood rather slim, that three sympatric species (*Nicrosaurus kapffi*, SMNS 12593, and "*Belodon plieningeri*"), of which the latter two are probably very similar in their ecological requirements, inhabited a geographically and environmentally restricted area.

Interpreting all characters in a very strict and restrictive sense, "*Belodon plieningeri*" must still be considered a metataxon sensu GAUTHIER (1986). The most applicable (and conservative) solution is to include all specimens in a single species of *Nicrosaurus*, which has yet to be formally named. The reduced thickness of the postorbito-squamosal bar is the only derived character state shared unequivocally by several specimens of the assemblage and thus tentatively suggested as an autapomorphy of the specimens formerly referred to "*Belodon plieningeri*". For reasons of

uninformative and potentially non-characteristic distribution, I do not propose the characters elongated squamosal body, pointed posterior process, and reduced width of supratemporal fenestra by means of an elongated parietal-supraoccipital complex with more gently sloping parieto-squamosal bar as autapomorphic for *Nicrosaurus* species B. If by future finds these three temporal characters of the low-domed morph SMNS 12593 will prove to be present in specimens referable to the high-domed morphs of *Nicrosaurus* species B like SMNS 4059 and BMNH 42745 as well, there might be a considerable number of apomorphic characters to distinguish *Nicrosaurus* species B from *Nicrosaurus kapffi*.

2.3.4.2 Variation of characters in *Nicrosaurus* species B and implications for their informativeness in phytosaur taxonomy and phylogeny

(1) High-domed and low-domed morphs

As in *Nicrosaurus kapffi*, two morphotypes can be recognised in *Nicrosaurus* species B. The low-domed morph is represented by SMNS 12593 and GPIT 2070.001. It must be noted, however, that SMNS 12593 obviously suffered from dorsolateral compaction, but its original skull height can still be estimated as somewhat less than GPIT 2070.001, and much less than the remaining specimens. SMNS 4059, BMNH 42745, and SMNS 12593/2 show a considerably narrower and higher skull (Tab. 2.3.1). Because of incomplete preservation, BMNH 39039 and SMNS uncat. no. 11 cannot be referred to either of the two morphs. The same dimorphism in the second species of *Nicrosaurus* substantiates the findings in *Nicrosaurus kapffi* and supports the underlying intraspecific rather than taxonomic variation or preservational bias.

The corresponding effects on the postorbital part of the skull are much the same as discussed for *Nicrosaurus kapffi*. In the high-domed morph of *Nicrosaurus* species B, the cheeks and the infratemporal fenestrae are steeper, the orbits are facing more laterally, and the paroccipital process of the opisthotic is more slender. High-domed specimens tend to have deeper palatal vaults (Tab. 2.3.1).

There are, however, a number of discrepancies when comparing the corresponding morphs of *Nicrosaurus kapffi* and *Nicrosaurus* species B. In *Nicrosaurus* species B, the postorbital part of the skull in the high-domed morph is increased in height not only relative to the width of the skull roof, but apparently also in absolute terms (Tab. 2.3.1). This becomes very obvious by comparing the occipital aspect of BMNH 42745 with SMNS 12593: in the high-domed first specimen (Fig. 2.59) the dorsoventral depth of the supraoccipital shelf is far greater than in the low-domed SMNS 12593 (Fig. 2.54). As far as can be said from the small sample size, the height of the skull is not coupled with a

characteristic snout profile or any other snout feature. Furthermore, the height of the skull does not go along with a particularly increased overall gracility of the specimen. Thus, in terms of general appearance, the two morphs of *Nicrosaurus* species B are more similar to each other than the more disparate morphs of *Nicrosaurus kapffi*. The high-domed and gracile *Nicrosaurus kapffi* BMNH 42743 is more "similar overall" to specimens of *Nicrosaurus* species B than to its conspecific morph.

(2) prenarial crest

The prenarial crest of *Nicrosaurus* species B is highly variable, both in terms of its presence among specimens referred to the taxon, but also regarding the shape of the structure.

In the specimens in which a prenarial crest is present, the length of the crest is remarkably constant. No specimen is known in which the prenarial crest extends beyond the midpoint of the snout, and this is in accord with the conditions in other taxa with partially crested specimens ("broken outline type" sensu MEHL 1916) as for instance *Arribasuchus*. Thus, the crested *Nicrosaurus* species B do not bridge the gap to *Nicrosaurus kapffi* regarding crest length. Although somewhat smaller, there is no reason to believe that the crested specimens of *Nicrosaurus* species B are "*Nicrosaurus kapffi* in the making".

In contrast to the always full developed height of the prenarial crest in *Nicrosaurus kapffi*, the specimens of *Nicrosaurus* species B show a gradual transition from crest-less to crested specimens, which might give insight into the development of the structure. The presence of a fully developed prenarial crest is actually independent from size among the sample of individuals. The specimens cannot be arranged in a meaningful size-related ontogenetic series regarding this character (Tab. 2.3.3). However, a prenarial crest must have been developed in the ontogeny of at least some specimens, and a recent report suggests that juvenile phytosaurs were indeed crest-less (HUNT *et al.* 1997). The different morphs of the prenarial crest may serve as a model for how the prenarial crest develops. The length of the prenarial crest in SMNS uncat. no. 11 corresponds exactly to the length of the slope of the snout in uncrested specimens. The condition in GPIT 2070.001 and SMNS 12593 is interpreted here as an intermediate stage between uncrested and crested examples of *Nicrosaurus* species B. Both specimens show still the normal, round-topped and sloping snout profile without significant elevation, while the dorsal section is already somewhat laterally constricted and offset from the base of the snout. This leads to a number of conclusions:

(a) The intermediate specimens underline that the sharp prenarial crest top is the derived character state, a polarity that can already be deduced from the shape of the snout in uncrested morphs.

(b) The crest develops predominantly by an upward growth of the whole snout area later becoming crested, rather than from posterior to anterior. Transferring this conclusion to *Nicrosaurus kapffi* means, that, if the juveniles of this species develop their crests during ontogeny as well, they can be expected to show full-length, but lower prenarial crests.

Table 2.3.3: Distribution of the prenarial crest and other skull characters in *Nicrosaurus* species B.

character	SMNS 12953	SMNS 4059	BMNH 42745	GPIT 2070.001	SMNS uncat. no. 11	BMNH 38039
skull length	610	[650]	[683]	[715]	?	?
prenarial crest	crested	crested	uncrested	crested	crested	uncrested
crest height	low	high	-	low	high	-
shape of crest top	round	sharp	-	round	sharp	-
morph	low-domed	high-domed	high-domed	low-domed	?	?
narial wing	present	present	present	absent	absent	absent

Abbrev.: [] estimated; ? unknown; - not present.

(c) Partially crested and uncrested specimens occur in the non-juveniles (using size as a criterion) of the same species, and there is no support from *Nicrosaurus* species B, that the presence of a partial prenarial crest is a taxonomic character at the species level. The polymorphism regarding crest presence, however, does not to my knowledge apply to taxa which include specimens with crests over the whole rostrum. This seems absolutely contradictory, but the full prenarial crest in *Nicrosaurus kapffi* may be advantageous or even necessary for functional reasons, especially when it is taken into account that the snout in this taxon is comparatively narrow in respect to other broad-snouted phytosaurs (*Angistorhinus megalodon*, *Smilosuchus gregorii*).

Regarding the partial prenarial crest, my interpretation differs from the taxonomic usage of GREGORY (1962a), BALLEW (1989), HUNT & LUCAS (1993c) and LONG & MURRY (1995). In the most thorough critique of crest variation and its underlying

reasons, BALLEW (1989) concluded that the taxonomic interpretation of presence/non-presence of phytosaur crests (including partial ones) is supported by a consistent distribution with other systematic characters. While I cannot fully assess the validity of BALLEW's (1989) claim in respect to North American forms, this is evidently not the case in *Nicrosaurus* species B. Therefore, I can only advocate a much more cautious approach to the use of the partial prenarial crest in phytosaur taxonomy.

The presence of a prenarial crest does not correlate with any of the character states suggested as sexually variable in *Nicrosaurus kapffi*. I cannot offer a satisfying explanation for the feature other than that the very restricted sample size may still distort the picture. In the specimens in which a fully developed and then sharp prenarial crest is present, the contour of the crest in a horizontal plane seems to vary individually, supporting an interpretation as a display structure. The cross-section of the prenarial crest in *Nicrosaurus* species B resembles closely the autapomorphic condition of *Arribasuchus buceros*, which was described as being "V-shaped" in BALLEW (1989; though exactly the same character state is given for *Arribasuchus mccauleyi*: p. 328).

(3) narial wing

The presence of a narial wing in only some specimens of *Nicrosaurus* species B shows that, in contrast to what might be concluded from the presence of the same condition in combination with the uniform profile of the posterior rostrum in *Mystriosuchus planirostris*, the character is not necessarily morphogenetically coupled with a steeply sloping posterior part of the snout. On the other hand, the presence of a narial wing in all specimens of *Mystriosuchus* known so far casts serious doubts on the interpretation of the character as sexually dimorphic in *Nicrosaurus* species B. There are also no obvious correlations with other osteologic features such as, for example, the shape of the crest or the width of the postorbital skull (Tab. 2.3.3).

The functional implications of the narial wing are at present unknown. In *Nicrosaurus* species B, the narial wing is always accompanied by two features: a triangular, flattened surface of the anterior narial rim which can be developed to a platform at the side of the nasal opening, and a groove along the naso-septomaxillary suture. As the narial wing, these structures represent most probably osteological correlates (see WITMER 1995, 1997) of soft tissue structures. The nature of such soft tissues is unknown, and to my knowledge no structure comparable to a narial wing is found in modern animals.

(4) anterior rim of supratemporal fenestra

In BMNH 42745 (Fig. 2.55) and SMNS 4059 (Fig. 2.45), the supratemporal fenestra seems to be reduced in the amount by which the opening indents the parietal and postorbital on the skull roof. Both specimens resemble *Nicrosaurus kapffi* in the round anterior rim of the fenestra. The parietal area medial to the supratemporal fenestra on the skull roof is damaged in SMNS 12593, but the extent to which the preserved remains project posteriorly is more in accord with *Nicrosaurus kapffi* (Fig. 2.48). This specimen is the only example of *Nicrosaurus* with a rectangular outline of the anterior supratemporal rim, showing an anterolateral notch into the postorbital. The varying length and shapes of the anterior part of the supratemporal fenestra in *Nicrosaurus* species B contrast with the more uniform individual development in *Nicrosaurus kapffi*. This may cast doubts on the validity of *Nicrosaurus* species B. Note, however, that there are slight variations in the better known taxon regarding the roundness of the anterior rim in SMNS 4379 (Fig. 2.8: oval) to SMNS 5726 (Fig. 2.15: almost subrectangular). The significance of these admittedly minor differences is difficult to assess, and I do not want to press taxonomic implications without better founded evidence. Some of the individual differences in the degree of indentation in the skull roof within *Nicrosaurus* species B may be attributed to poor preservation in particular specimens. With the exception of *Nicrosaurus kapffi*, the variation of these characters in other phytosaur taxa regarded as valid has never been documented. However, similarly dimorphic anterior borders of the supratemporal fenestrae were reported among the specimens referred to *Rutiodon carolinensis* (DOYLE & SUES 1995), and the authors also suggested some variation among non-phytosaurid phytosaurs.

(5) supraoccipital and foramen magnum

In SMNS 12593 and BMNH 42745, the supraoccipital reaches the foramen magnum but participates in bordering the foramen over a much smaller distance only. *Nicrosaurus* species B thus show a condition mediating between the two stages described in part 2.2.7.1 (29) for *Nicrosaurus kapffi* SMNS 4378 and 4379 (supraoccipital roofs foramen magnum), and SMNS 5726 (supraoccipital excluded from foramen magnum). GOWER & SENNIKOV (1996) discuss the utility of this character at genus level within the higher category Archosauria, and conclude that the phylogenetic value of the amount, by which the supraoccipital borders the foramen magnum is questionable. The polymorphy within the genus *Nicrosaurus* underlines the uninformativeness of the character.

2.3.4.3 Non-diagnostic distinguishing characters between *Nicrosaurus* species B and *Nicrosaurus kapffi*

The diagnostic characters of both species as determined above are usually not preserved in fragmentary material, and also in a number of more complete *Nicrosaurus* skulls. The fact that in the high-domed, gracile morphs of *Nicrosaurus kapffi*, especially in BMNH 42743, a number of characters are developed in a condition seen in most, if not all specimens of *Nicrosaurus* species B, renders a clear distinction especially between the high-domed morphs of both species almost impossible as long as the specimens are not completely preserved. Indeed, if *Nicrosaurus kapffi* did not have a discrete and unique crest morphology, and if two morphs could not be fairly well distinguished in both taxa, a single species of *Nicrosaurus* with dimorphic crest length and morphological gradation in many skull features probably would have been the most parsimonious interpretation. It is thus desirable to establish, or at least propose, a set of distinguishing characters apart from the suggested diagnostic features. The question is whether such a list will prove useful in practice.

A list of disparate characters in *Nicrosaurus* is presented in Table 2.3.4. The characters are subdivided into two categories. The first category shows two discrete and clearly distinguishable character states, and it is obvious that only such characters are of practical value. Note, however, that these characters cannot be proposed as apomorphic or diagnostic, since the character state may be primitive, the polarity of the character transformation may be unknown, or the distribution of the character states among the specimens is not unequivocal, i.e. the competing character state may occur in the same species as well. The character states with a high degree of informativeness and which are empirically estimated as useful for a species determination, are marked with asterisks. The meaning of such characters is, that a specimen in which it is expressed belongs with reasonable certainty to this taxon; however, absence does not necessarily allow a referral to the other.

Unfortunately, at the present state of knowledge, the majority of the distinguishing characters between both species of *Nicrosaurus* are characters, in which the characters states form a continuum. These include mainly the proportional development of a single character or a particular structural complex. Discrete character states in such features are always difficult to define objectively, since they represent gradual rather than stepwise transformations. Note that the ambiguity of some character states might be a result of deformation or of the small sample size, preventing a meaningful clustering in two statistically discrete character state groups. Size or "robusticity" of specimens may play an important role as well: some of the characters involved may be attributed to the effects

Table 2.3.4: Disparate discontinuous and continuous character states in *Nicrosaurus*.

#	character description	*Nicrosaurus* species B character state	*Nicrosaurus kapffi* character state
discontinuous characters or available discrete character states			
1	dentition: number of sets	bipartite, without premaxillary set*	tripartite, with premaxillary set*
2	narial wing: presence	present*	absent
3	naris opens into groove along naso-septomaxillary suture:	present*	absent
4	septomaxilla: anterior extend	terminates at level of nasal tip*	terminates anterior to nasal*
5	septomaxilla: shape of anterior part	one prong	multi-pronged *
6	maxillo-nasal suture: course	enters antorbital fenestra	above antorbital fenestra*
7	lateral face of maxilla: slope	almost vertical	slopes ventrolaterally*
8	internal antorbital opening: presence	present*	absent
9	squamosal: shape of medial rim of posterior process	angular	parabolic*
10	squamosal: flattened surface posteromedial	absent	present
11	squamosal: shape of tip of posterior process	pointed*	broadly rounded*
12	squamosal: ventrally pointing knob	absent*	present*
13	squamosal: lamella onto posterior face of paroccipital process bordering posttemporal fenestra ventrolaterally	absent	present*
14	squamosal: lamina onto anterior face of paroccipital process	unknown	present*
15	supratemporal fenestra: anterior rim	rectangular*	rounded
16	supraoccipital: borders foramen magnum	at centre of roof	absent
17	paroccipital process: anteroposterior extension of lateral part	strongly compressed anteroposteriorly*	expanded, shelf in front of the ventral opisthotic ridge
18	opisthotic lamella: shape	broad and blunt*	sharp
19	pteroccipital fenestra: shape	medially expanded in anterior part and narrowed to slit posteriorly*	uniform slit-like
20	short ridge on anteriormost border of pteroccipital fenestra:	present*	absent
21	ectopterygoid groove	present*	absent
continuous characters without discrete character states			
22	skull length in non-juveniles	smaller (610 - 715 mm; Ø 650 mm)	larger (730 - 920 mm; Ø 795 mm)
23	premaxillary teeth: setting	set more laterally visible in lateral view	set more ventrally, not visible in lateral view
24	preorbital part of skull: sculpture	more prominent	less prominent
25	foramina at tip of snout	numerous	less numerous
26	raised dorsal orbital rims resulting in interorbital depression	present	absent
27	parietal: width of supraoccipital lamina of squamosal process	more extensive over posterior part of supraoccipital shelf	less extensive
28	parietal: overhang of proximal part of squamosal process	strong	less strong
29	parietal: groove in middle section of the squamosal process	present	less developed or absent
30	parietal: slope of dorsal rim of squamosal process	more gently	more steeply

Table 2.3.4 (continued)

31	squamosal: length	elongated	not elongated
32	squamosal: length of quadratojugal process	visible along half of rim of infratemporal fenestra or more	visible along half of rim of infratemporal fenestra or less
33	squamosal: thickness of postero-medial rim of posterior process	not considerably thickened	greatly thickened
34	squamosal: size of paroccipital process	small	large
35	supratemporal fenestra: insertion into skull roof	shallow	deeper
36	supratemporal fenestra: constricted posteriorly	present	absent
37	quadratojugal: lateral depression	present	absent
38	quadratojugal-jugal bar: ventral rim	thin and sharp-edged	thick and round
39	alveolar ridges: visibility	more prominent, visible in lateral view	less prominent
40	anterior part of vomers: width	slender	expanded to rhombic shape
41	ventral aspect of pterygo-quadrate bar: grooves	less well developed or absent	well developed
42	lateral condyle of quadrate: distinctiveness	offset from cheek, in extreme with vertical step	not markedly offset from cheek
43	craniomandibular joint of quadrate: size	less wide and more slender	wide and broad
44	supraoccipital shelf: shape	elongated and narrow	short and broad
45	posterior edge of supraoccipital shelf: development	prominent	less prominent
46	paroccipital process: cross-section of medial part	dorsoventrally compressed, with ridge on posterior face	cylindrical, ridge less well developed
47	ventral surface of basal tubera: orientation	facing more posteriorly than posteroventrally	facing posteroventrally
48	basioccipital: contribution to ventral surface of basal tubera	occupies c. 25% of ventral surface	occupies up to 50% of ventral surface
49	basal tubera: shape	narrower anterioposteriorly, stronger laterally expanded	broader anterioposteriorly, less laterally expanded
50	basipterygoid process: shape	longer and less splayed	stout and more splayed
51	basisphenoid corpus: width	strongly constricted	slightly constricted

of scaling when a generally gracile built skull (*Nicrosaurus* species B) is compared with a more robust one (*Nicrosaurus kapffi*). Such characters are of little usefulness alone, but may support a decision if discrete characters are not fully decisive.

The problem with non-autapomorphic characters is well illustrated by BMNH 38037, the well preserved posterior part of a high-domed skull, which includes the dorsal side of the left narial region and the braincase completely freed from matrix. The diagnostic characters of *Nicrosaurus* and also of the two species are not preserved, but the specimen conforms to the general skull anatomy of *Nicrosaurus*.

Six discrete character states in BMNH 38037 suggest a referral to *Nicrosaurus* species B, but are possibly affected by the preservation or are combined with contradictory character states. The anterior part of the narial rim slopes down and merges

with an horizontal area just lateral to the tip of the naris. The presence of such a narial wing (#2 of Table 2.3.3) would be a compelling discrete character, since it never occurs in *Nicrosaurus kapffi*. However, whereas the slope of the rim seems to be genuine, the horizontal part of the narial rim clearly exhibits internal bone tissue. It is impossible to decide whether the whole excavation of the anterior narial rim is genuine, or merely represents an artefact. Secondly, the profile of the postorbital snout is somewhat sloping (plesiomorphic state of the autapomorphy of *Nicrosaurus kapffi*), but is very incompletely preserved and the descent could be strongly accentuated by deformation. Thirdly, the posterior process of the squamosal is very similar in shape to SMNS 12593 in being angular (#9) and pointed (#11); however, the first character is not absolutely diagnostic because it also occurs in *Nicrosaurus kapffi* SMNS 5727, and there are a number of other squamosal characters that point toward *Nicrosaurus kapffi*. Fourthly, the skull lacks the flattened posteromedial surface of the posterior process of the squamosal (#10), but this is also the case in one *Nicrosaurus kapffi* (SMNS 5726). There is no ventrally pointing knob on the ventral surface of the posterior process of the squamosal (#12). This character state seems to be confined to *Nicrosaurus* species B. Lastly, the squamosal does not extend onto the paroccipital process (#13).

The skull shows further affinities to *Nicrosaurus* species B in having a deeply saddle-shaped orbito-nasal region (#26), a pronounced depression in the ventral part of the quadratojugal (#37), a sharp quadratojugal-jugal bar (#38) and a transversely more slender and comparatively wider craniomandibular joint of the quadrate which is also offset from the cheek laterally (#42, 43). Also, the supraoccipital shelf is posteriorly expanded and horizontally deflected (#44), and the basal tubera face more posteroventrally (#47).

On the other hand, these characters are contradicted by features that suggest a specimen of *Nicrosaurus kapffi*: the supraoccipital forms the entire roof of the foramen magnum (#16); the sculpture of the narial region is not particularly deep (#24); the wide supratemporal fenestrae cut deep into the skull roof and are rounded anteriorly (#35, 15); the squamosal process of the parietal is steep (#30), without a distinct groove in middle section (#29), and does not extend far onto the supraoccipital shelf (#27); the overhang of the parietal over the supraoccipital shelf is not marked (#28); the paroccipital process of the squamosal is very large (#34), reaching 25% of the skull height; the extremity of the opisthotic is somewhat compressed anteroventrally, but not as much as in SMNS 12593, and shows a clearly distinguished shelf (#17); the squamosal is not elongated, its quadratojugal process is short, and the posteromedial rims are thickened (#31-33); the pterygo-quadrate bar shows well developed grooves (#41); the base of the paroccipital process of the opisthotic is high, cylindrical, and lacks a posterior ridge (#46); the

characters of the basisphenoid (#48-51) correspond with *Nicrosaurus kapffi*. A particularly important observation is the thick, *Nicrosaurus kappfi*-like postorbito-squamosal bar. BMNH 38037 is another reason why my assessment of this character state as diagnostic for *Nicrosaurus* species B is very tentative.

Several feature of BMNH 38037 have not been identified in *Nicrosaurus* so far. These include the enormous enlargement of the paroccipital process of the squamosal, a greatly dorsoventrally expanded vertical side of the squamosal (30% of skull height) that is higher than in any other specimen of *Nicrosaurus*, and a considerably shorter posterior process reaching a length behind the paroccipital process of the opisthotic of only 9 mm. Furthermore, there is a distinct, horizontal ledge of the parietals that overhangs the supraoccipital shelf. The parietal-supraoccipital complex clearly lacks the parietal groove of *Nicrosaurus kapffi* linking the skull roof with the supraoccipital shelf. There is no evidence available against a similar ledge in *Nicrosaurus* species B. The thickness of the opisthotic lamella (#18) is inconclusive in the specimen, being very broad on the right-hand side, but thin and sharp on the left.

In conclusion, BMNH 38037 is identified as *Nicrosaurus* based on its overall shape only, but it is impossible to refer the skull to a species. 17 characters states argue for a referal to *Nicrosaurus* species B, of which three have been demonstrated for this species only. On the other hand, there are 20 character states in accord with *Nicrosaurus* kapffi, but all of them can be found in individuals of *Nicrosaurus* species B or the character state is known from one specimen only. I tend to regard the specimen as a high-domed *Nicrosaurus* species B, in particular because of the possible presence of a narial wing, the angular and pointed posterior process of the squamosal that lacks a ventral protuberance, and the parietal ledge. However, a number of characters conflict with such an identification, and some of the *Nicrosaurus* species B character states come close to the condition in the gracile *Nicrosaurus kapffi* SMNS 42743. The thick postorbito-squamosal bar points towards a high-domed specimen of *Nicrosaurus kapffi*, and was the decisive reason for not assigning the specimen to *Nicrosaurus* species B.

Despite BMNH 38037 showing the most complete braincase available of a *Nicrosaurus*, and potentially being the best preserved posterior skull of a *Nicrosaurus* species B, it is not considered in the descriptions of that species. The specimen demonstrates that, if the diagnostic characters of *Nicrosaurus kapffi* (or their corresponding plesiomorphic state) cannot be determined for preservational reasons, an identification at species level is extremely difficult in *Nicrosaurus*. This might well apply to phytosaurs in general, and it underlines the importance of defining and using unequivocally diagnostic (autapomorphic) characters in phytosaur alpha-taxonomy.

SMNS 12593/2, a strongly laterally compressed skull fragment which is lacking most of the rostrum and the whole postorbital part of the skull, from Weißer Steinbruch near Pfaffenhofen, is difficult in another way. The specimen shows strong affinities with *Nicrosaurus* species B, but it is problematic because there are at least two character states present that are similar to, or approach the condition seen in *Mystriosuchus*.

SMNS 12593/2 possesses one diagnostic character of *Nicrosaurus*, the infranasal recess, and corresponds to *Nicrosaurus* species B in having a gently sloping prenarial section of the rostrum. In contrast to *Mystriosuchus planirostris*, the narial septum is not rectangular in shape, but straight and constantly sloping anteriorly over its whole length, and the posterior part of the nasal opening does not face exactly dorsally, but is inclined anteriorly and aligned with the anterior part. SMNS 12593 also lacks a number of additional characteristics of both *Mystriosuchus*, notably the conspicuously deeper sculpture on top of the narial region as well as the deep preorbital depression.

However, the most striking feature of SMNS 12593/2 is a large, 30 mm long, and ovoid pre-infratemporal shelf, which otherwise is only shared by specimens referable to the two species of *Mystriosuchus*. The specimen also shows a much more prominent narial wing than any specimen of *Nicrosaurus* species B. The development of the wing separates the narial rim into a gently sloping posterior third, which faces anterodorsally, whereas the anterior two thirds of the rim is deeply excavated and depressed, leaving much of the internasal septum well exposed in lateral view.

In summary, SMNS 12593/2 has both a synapomorphy of *Nicrosaurus* (infranasal recess) and *Mystriosuchus* (pre-infratemporal shelf). Since no *Mystriosuchus* shows an infranasal recess, but SMNS 12593 and GPIT 2070.001 also have a shallower and larger pre-infratemporal recess compared to other *Nicrosaurus* species B and all *Nicrosaurus kapffi* (Figs. 2.47, 2.62), SMNS 12593/2 is tentatively referred to *Nicrosaurus* species B.

Chapter 3

Mystriosuchus

Section 3.1
The genus *Mystriosuchus* E. FRAAS, 1896

3.1.1 Systematic palaeontology

Archosauria COPE, 1869

Crurotarsi SERENO et ARCUCCI, 1990

Phytosauria JAEGER, 1828 (*sensu* DOYLE & SUES 1995)

Phytosauridae JAEGER, 1828 (*sensu* DOYLE & SUES 1995)

Genus *Mystriosuchus* E. FRAAS, 1896

Type species: *Mystriosuchus planirostris* (MEYER, 1863), by indication in FRAAS (1896) in accord with Art. 68(d) ICZN (monotypy)

Species included: unnamed species, here referred to as *Mystriosuchus* species B

Synonyms: *Belodon* MEYER, 1844

Summary description (diagnostic characters excluded): highly derived clade of medium to large-sized Phytosauria (skull length 800 to >1000 mm); snout slender and greatly elongated (ratio prenarial to narial + postnarial skull length 2.2 - 2.7); no prenarial crest, but a premaxillary crest may occur; naris at level of or below the skull roof; anterior rim of the naris at level of the anterior rim of the antorbital fenestra; narial wing always present; postorbital part of the skull narrow, high, and anteroposteriorly abbreviated; quadrate foramen large; postorbito-squamosal bar broad, thick and triangular in cross-

section; postorbito-squamosal bar hangs very slightly over the supratemporal fenestra, which is fully open dorsally; strong lateral ridge on the postorbito-squamosal bar; quadratojugal process of the squamosal extends along the entire posterior rim of the infratemporal fenestra; posterior process of the squamosal very short or not developed; extremity of the posterior process not broadly rounded; dorsal recess covers entire ventral surface of the squamosal; parieto-squamosal bar closely appressed on the paroccipital process of the opisthotic; ventral sulcus reduced to a narrow fissure; parieto-squamosal bar greatly depressed below the level of the skull roof by at least 25% of the skull height; well developed parietal ledge present; parietal-supraoccipital complex high, anteroposteriorly abbreviated, and dorsally rounded; no extended lamina of the squamosal process of the parietal onto the supraoccipital shelf; posttemporal fenestra positioned under the central third of the posterior rim of the supratemporal fenestra; lateral half of the paroccipital process subrectangular, facing posterodorsally in occipital aspect; no furrow on the deflected part of the pterygo-quadrate plate; quadrate wing of the pterygoid bifurcated; well-demarcated ventral ridge on the paroccipital process; ventral surface of the basal tubera small, suboval in shape, and directed almost exactly ventrally; dentition bipartite.

Since in the specimen GPIT 261/001 (*Mystriosuchus* species B) numerous skull characters are preserved in much more detail than in the available skulls of *Mystriosuchus planirostris*, I refer to the description of this taxon rather than that of the type species regarding the general characteristics of a *Mystriosuchus* skull.

Suggested diagnostic characters (see discussion in subsection 3.1.2):

(1) ratio of rostral to narial and postnarial length is > 2.2.

(2) interpremaxillary fossa reduced to a slit in the anterior part of the premaxilla.

(3) deep sculpture of the skull roof and the narial region.

(4) presence of a preorbital depression.

(5) well-demarcated, anteroposteriorly wide pre-infratemporal shelf.

(6) anterior border of the supratemporal fenestra raised.

(7) dorsoventrally thick parieto-squamosal bar with a triangular cross-section

(8) posttemporal fenestra extremely reduced.

(9) squamosal process of the parietal descends vertically.

Distribution: central Europe: Southwest Germany, Austria, northern Italy.

Stratigraphic range: Upper Triassic; Germany: Keuper succession, Middle Keuper, Stubensandstein, middle Stubensandstein, sandstone subunits sc2 and sc3; Austria: Dachsteinkalk; Italy: Dolomia Principale, Calcare di Zorzino Formation.

Age: Middle (and Lower?) Norian, Late Triassic.

3.1.2 The diagnostic characters of *Mystriosuchus*

In this section, the characters identified as diagnostic for *Mystriosuchus* are listed and discussed. For convenience, the complementary state of each character state pair is given in parenthesis.

3.1.2.1 Suggested diagnostic characters

(1) extremely long prenarial snout (regarding other Phytosauridae), the ratio of rostral to narial and postnarial length being > 2.2 (GREGORY 1962a: character 9; CHATTERJEE 1978); [ratio distinctly below 2, see Appendix B, Tab. B1].

(2) interpremaxillary fossa reduced to a narrow slit in the anterior part of the premaxilla by a close approximation of the alveolar ridges; [interpremaxillary fossa continuously broad].

The close approximation of the alveolar ridges in *Mystriosuchus* species B is demonstrated in Figure 3.10. In the German specimens of *Mystriosuchus planirostris* that show a complete snout, the mandibles are either preserved in occlusion with the snout (SMNS 9134, SMNS 13007, SMNS 13240), or the palate is not freed from matrix (HMB MB.I.008.05, FSF unnumb., GPIT 249/002). The palatal aspect of the anterior premaxillae is thus obscured from view. The derived character state similar to *Mystriosuchus* species B is visible, however, in MBSN 2 (PINNA 1987: fig. p. 70; RENESTO & PAGANONI 1998: fig. 1).

In most phytosaurs with comparable slender snouts, the interpremaxillary fossa remains a broad-roofed structure over the whole length of the premaxillae. This condition is illustrated here for *Nicrosaurus* species B in Figure 2.56, but applies also to *Francosuchus*, *Paleorhinus*, "*Parasuchus*", and *Pseudopalatus* (KUHN 1936: pl. 8 fig. 1b, pl. 11 fig. 4; DUTUIT 1977b: pl. 1C; CHATTERJEE 1978: pl. 8b; MEHL 1928b: fig.

23B). CASE (1922: pl. 11 fig. C) figured *Promystriosuchus* with a *Mystriosuchus*-like interpremaxillary fossa, but according to the poor preservation of the type specimen (HUNT & LUCAS 1991; LONG & MURRY 1995: fig. 23B), the shape of the fossa is largely reconstructed.

(3) deep sculpture of the skull roof and the narial region with emphasised concavities (WESTPHAL 1963b; GREGORY & WESTPHAL 1969; HUNT & LUCAS 1989b); [less deep sculpture with emphasised convexities].

The system of anastomosing deep pits and vermiculate blunt ridges on the skull roof, the area between orbits and nares, and below the nares is unique among phytosaurs, both regarding the type and the development of the surface ornamentation. In contrast to the skull ornamentation in other phytosaurs, the concave elements of the sculpture (pits) are particularly emphasised and dominate visually over the elevated components (ridges, knobs) in *Mystriosuchus*.

(4) presence of a preorbital depression; [preorbital depression absent].

(5) presence of a well-demarcated, anteroposteriorly wide pre-infratemporal shelf; [small, but deep pre-infratemporal recess, or high and narrow pre-infratemporal shelf].

Mystriosuchus shows a flat, unsculptured area in front of the anteroventral corner of the infratemporal fenestra framed by a prominent horizontal ventral and a posterodorsally trailing anterior ridge. This area is called here the pre-infratemporal shelf. The shelf covers most of the postorbital process of the jugal and extends far anteriorly (maximum observed length is 30 mm) reaching almost the antorbital opening. This contrasts with most other phytosaurs, in which the pre-infratemporal shelf is either considerably smaller (e.g. *Nicrosaurus* species B, but see part 2.3.4.3) or is represented by a small, but deep crescentic recess (e.g. *Nicrosaurus kapffi*, section jugal in part 2.2.3.3). *Pseudopalatus pristinus* (BALLEW 1989: pl. 8 fig. C; Long & Murry 1995: fig. 41A) and *Arribasuchus buceros* (BALLEW 1989: pl. 8 figs. B, D) show also a conspicuous pre-infratemporal shelf, but in these taxa the shelf is a narrow strip paralleling the anteroventral rim of the fenestra compared to the broad shelf of *Mystriosuchus*.

(6) anterior border of the supratemporal fenestra raised; [anterior border of the supratemporal fenestra at level with the surrounding skull surface].

The character state applies to both species of *Mystriosuchus*, and is a unique character for this genus. *Mystriosuchus planirostris* can be distinguished form

Mystriosuchus species B by the extension of the raised border all along the lateral rim of the supratemporal fenestra (part 3.2.3.1)

(7) postorbito-squamosal bar thick and triangular in cross-section; [thin, medially extending lamella of the squamosal over the supratemporal fenestra].

Previous descriptions of the postorbito-squamosal bar in phytosaurs do not comment explicitly on the thickness of this structure. *Nicrosaurus* shows a thin medial lamella combined with a much less thicker vertical section of the squamosal, and probably the same is the case in *Pseudopalatus* and *Arribasuchus*. *Smilosuchus* lacks such a medial lamella, and the vertical part of the squamosal is a comparatively thin structure with an essentially even thickness throughout its height (pers. obs.) rather than thickened dorsally to achieve the typical cross-section of *Mystriosuchus*. This might suggest that the same is the case for the closely related *Leptosuchus*. No information can be derived from the literature for taxa which are more primitive than *Smilosuchus* (Angistorhininae, non-phytosaurid phytosaurs). As long as there is no evidence to the contrary, I regard the massive triangular postorbito-squamosal bar of *Mystriosuchus* as diagnostic for the genus.

(8) posttemporal fenestra extremely reduced both in terms of height and width (GREGORY 1962a; CHATTERJEE 1978); [posttemporal fenestra are much higher and cover at least one half of the width of the parieto-squamosal bar].

The greatly reduced width of the posttemporal fenestra of *Mystriosuchus* is unparalleled among phytosaurs. This is probably the result of the greatly depressed parieto-squamosal bar. The size reduction is also expressed in the unusual placement of the fenestra above the central third of the paroccipital process, rather than above the medial half as in the majority of phytosaurs.

(9) squamosal process of the parietal descends vertically (modified after BALLEW 1989: character 63); [squamosal processes of the parietal slopes steeply downward].

BALLEW's (1989: 314) autapomorphic character 63 for *Mystriosuchus* reads "parietal-supraoccipital complex is more compressed than seen before". However, it proved impossible to demonstrate such a compression quantitatively based on the available published sources. For this reason, the character is redefined here in terms of an unambiguous character state. *Arribasuchus* and *Pseudopalatus* show broadly similar shaped parietal-supraoccipital complexes, but in these genera the squamosal processes of the parietals are not vertical, but steeply sloping, which leads to a broader supraoccipital shelf.

3.1.2.2 Rejected previously suggested diagnostic characters and autapomorphies

(i) rostrum dorsoventrally flattened to a high degree, resulting in a subrectangular cross-section.

The character state that inspired MEYER (1863) to choose the species name of the type species, is well developed in all *Mystriosuchus planirostris* in which the snout is at least partially preserved, as well as in *Mystriosuchus* species B GPIT 261/001. It is not uncommon that the rostrum in phytosaur taxa with slender snouts is wider than high (e.g. KUHN 1936). However, in all these forms (*Ebrachosuchus*, *Francosuchus*, "*Parasuchus*", *Paleorhinus*, *Promystriosuchus*, *Rutiodon*, *Pseudopalatus*) the dorsal surface of the rostrum remains primitively rounded, i.e. semicircular in cross-section, rather than flat and horizontal. The only exception is represented by *Nicrosaurus* species B SMNS 12593 showing the same flattened morphology of the anterior part of the rostrum (Fig. 2.52), although the flattening in this specimen may be exaggerated by dorsoventral compaction. Hence, *Mystriosuchus* (*planirostris*) and *Nicrosaurus* species B are not necessarily distinguishable based on the shape of the rostrum alone (e.g. SMNS uncat. no. 2, section 3.2.1). This leaves the character principally unsuitable as diagnostic character for *Mystriosuchus*.

(ii) rostrum low and slender, sometimes bearing a local dorsal swelling (GREGORY 1962a: character 8, 1969; GREGORY & WESTPHAL 1969; CHATTERJEE 1978).

Low and slender rostra are characteristic of numerous other taxa (all non-phytosaurid phytosaurs, *Rutiodon carolinensis*, *Pseudopalatus pristinus*). Moreover, it is almost certainly the primitive character state within Phytosauria (DOYLE & SUES 1995). The "local dorsal swelling" is most likely a characterisation of the premaxillary crest of *Mystriosuchus* species B, which is discussed in part 3.3.4.2, (3).

(iii) orbits directed more outward than upward (LONG & MURRY 1995; GREGORY 1962a: character 6; CHATTERJEE 1978).

Although the character is principally questioned by the variation seen within other species such as *Nicrosaurus kapffi* (part 2.2.7.1, (18); part 2.2.7.3) and *Nicrosaurus* species B (part 2.3.4.2) and genera (*Paleorhinus*, see CASE 1922; CHATTERJEE 1978; DUTUIT 1977a), the statement is correct for all known specimens of both *Mystriosuchus* species. However, the same is also characteristic of *Pseudopalatus pristinus*.

(iv) parietal forms a distinct ledge over the supraoccipital shelf (BALLEW 1989: character 64).

BALLEW (1989: character 64) introduced the presence of a ledge above the supraoccipital shelf as the posteriormost extension of the parietals as an autapomorphy of *Mystriosuchus*. Firstly, this is essentially a more derived second state of her character (42) "parietals form an overhang over the supraoccipital", which was incorrectly identified as synapomorphy of *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus* (see subsection 5.3.2, (24)). More importantly, there is a definitely a problem in defining the threshold between an "overhang" and a "ledge". *Mystriosuchus* contrasts with less derived phytosaurs such as *Nicrosaurus kapffi* and *Nicrosaurus* species B in having a transverse horizontal rim of this overhang rather than a triangular shaped roof. In comparison to *Pseudopalatus* and *Arribasuchus* , the ledge is more conspicuous in *Mystriosuchus* because it is thickened and appears somewhat longer. These differences might be considered diagnostic. However, the development is not uniform within *Mystriosuchus* (the ledge of *Mystriosuchus* species B resembles more that seen in *Pseudopalatus pristinus* than *Mystriosuchus planirostris*), and a distinction of character states is subjective. A comparable prominent horizontal ledge is also not restricted to *Mystriosuchus*, but has also been figured in all angistorhinine phytosaurs (CASE & WHITE 1934: pl. 8 fig. 2; DUTUIT 1977a: fig. 2B, fig. 3; MEHL 1915: fig. 5).

(v) quadrate rather tall (GREGORY 1962a: character 2, 1969; similar wording in LONG & MURRY 1995; CHATTERJEE 1978).

The definition of the character by GREGORY (1962a) is precise enough to synonymise the character state with either a high postorbital part of the skull or less laterally splayed cheeks. Both features have been shown to be intraspecifically variable in *Nicrosaurus kapffi* (part 2.2.7.1, (23); part 2.2.7.3), *Nicrosaurus* species B (part 2.3.4.2, (1)), and possibly *Smilosuchus gregorii*, and the alpha-taxonomic utility is principally questionable. In contrast to these examples, the character state seems to be stable in *Mystriosuchus*. Nevertheless, a similar tall quadrate occurs also invariably in specimens of *Pseudopalatus pristinus*.

(vi) dentition: teeth slender and not enlarged posteriorly, round with weakly developed keels to slightly compressed (GREGORY 1962a: character 10).

The character descriptions applies perfectly to *Mystriosuchus planirostris*. However, the dentition is virtually unknown for *Mystriosuchus* species B. Circumstantial evidence in this species suggests that the teeth are size-differentiated and it is likely that

these teeth differ also in morphological characters (part 3.3.2.1). It is thus doubtful whether the characters listed by GREGORY apply to the genus *Mystriosuchus*.

In redefining the subfamily Mystriosuchinae HUENE, 1915, LONG & MURRY (1995) suggested a set of autapomorphic characters for this taxon. Since LONG & MURRY's Mystriosuchinae is monotypic in contrast to Mystriosuchinae *sensu* CHATTERJEE (1978), these characters represent in fact an autapomorphic characterisation of the genus *Mystriosuchus*. However, the validity of most of these characters, listed under topics (vii) to (xi) below, depends entirely on the acceptance of LONG & MURRY's suggested phylogenetic hypothesis claiming that *Mystriosuchus* represents a sistergroup of the basal group "Paleorhininae". Similarly, the acceptance of character 62 suggested autapomorphic for *Mystriosuchus* by BALLEW (1989) relies on the validity of the sistergroup relationship between *Mystriosuchus* and *Pseudopalatus pristinus* (topics xii to xiii). The groups which later form the basis of a phylogenetic analysis (morphospecies or genera) need to be defined *a priori* independently from any phylogenetic assumptions. In the absence of an undisputed phylogenetic framework, only these characters can be primarily accepted as diagnostic that are (1) derived regarding a non-phytosaurian outgroup and (2) unequivocally distributed, meaning derived character states shared uniquely by the individuals in question. Shared plesiomorphic characters states cannot be identified as reversals without the context of a phylogenetic hypothesis. Apomorphic characters, which are shared with individuals not included in the operational taxonomic unit, do not indicate *a priori* whether they have been acquired independently or are potentially synapomorphic for a larger group (i.e. plesiomorphic at the level of the operational taxonomic unit), and are not accepted here at the initial stage of an analysis. However, such characters may be informative and identified as synapomorphic at a stage when a phylogenetic hypothesis has been formulated and proved robuster than competing hypotheses (see part 5.4.3.2).

(vii) external nares above the antorbital fenestra (LONG & MURRY 1995; GREGORY 1962a: character 1).

(viii) postorbito-squamosal bar wide (LONG & MURRY 1995).

According to LONG & MURRY's own data, the same character state applies also to *Nicrosaurus*, *Pseudopalatus* and *Arribasuchus*.

(ix) supratemporal fenestra greatly depressed (LONG & MURRY 1995; GREGORY 1962a).

The relative figure of the depression of the parieto-squamosal bar below the skull roof in one species, *Mystriosuchus* species B, overlaps with the degree seen in *Pseudopalatus* and *Arribasuchus* (Appendix B, Tab. B4). The character is thus not diagnostic for the genus *Mystriosuchus*. The assessment of the character state as autapomorphy of the genus relies, again, on the hypothesis that *Mystriosuchus* forms a clade with "Paleorhininae".

(x) paroccipital process of the squamosal moderately large and hooked (LONG & MURRY 1995).

The polarity of the character (size increase) only applies when *Mystriosuchus* is included within Mystriosuchidae *sensu* LONG & MURRY (1995). The size of the process in both species of *Mystriosuchus* falls within the size range seen in numerous other phytosaur taxa. Furthermore, the actual shape of the process in *Mystriosuchus* does not match the term "hooked", but is either irregular or rhomboidal in lateral view. I do not see significant shape differences from many other phytosaurs.

(xi) interpterygoid vacuity small (LONG & MURRY 1995; GREGORY 1962a: character 11; GREGORY & WESTPHAL 1969; CHATTERJEE 1978).

(xii) truncated posterior process of the squamosal (BALLEW 1989: character 62; GREGORY 1962a: character 4; GREGORY & WESTPHAL 1969; CHATTERJEE 1978).

(xiii) well-defined ridge on the lateral border of the upper temporal bar (GREGORY 1962a: character 5).

The significance of this character and the distribution among Phytosauria is further discussed in subsections 5.3.1 (10) and 5.3.2 (29). The same character state is definitely present at least in the non-phytosaurid phytosaurs, and has been put forward to substantiate a close relationship of *Mystriosuchus* with "*Paleorhinus*" (GREGORY 1962a; BALLEW 1989; LONG & MURRY 1995). It is therefore not *a priori* diagnostic for *Mystriosuchus*.

Section 3.2
Mystriosuchus planirostris (MEYER, 1863)

3.2.1 History of taxonomy and research

The first report of a vertebrate fossil from Aixheim was a tooth derived from the "Stubensandstein from the Hegau region" in the collection of Baron von ALTHAUS (MEYER & PLIENINGER 1844: 44, 85). Later figured and distinguished as an unnamed genus different from *Belodon* (MEYER 1847-55: 148, pl. 20 fig. 5), it is now readily identifiable as a tooth of *Mystriosuchus planirostris*. In the following years, the collections in Stuttgart and Tübingen occasionally acquired fragmentary vertebrates from the Aixheim quarries (QUENSTEDT 1882-85; GPIT archives; SMNS archives). The majority of material apparently found its way into private collections (ALBERTI 1864; ESER 1862, 1907; PLIENINGER 1857). According to these reports, however, these remains consisted mostly of indeterminable phytosaur and prosauropod postcrania, and teeth of phytosaurs and other archosaurs. After some years of fruitless efforts, the private collector and then well established amateur naturalist Friedrich ESER managed to get hold of a partial phytosaur skull, most probably from a quarry at Neuhaus (ESER 1862, 1907). The specimen was described in MEYER's series of monographs on Keuper tetrapods and received the name *Belodon planirostris* (MEYER 1862, 1863). Although the specimen was very fragmentary, MEYER was able to distinguish the new species from "*Belodon*" *kapffi* and "*Belodon*" *plieningeri* not only by the dorsoventrally flattened snout, but stressed also two characters interpreted as diagnostic here, the steeply sloping prenarial area and the subdivision of the naris into a horizontal and subvertical part, mentioning the protruding internasal septum as well. His description was vindicated by HUNT & LUCAS (1989b) after they had relocated the type material at the Museum of Comparative Zoology at Harvard University.

For more than 30 years, no more finds of *Mystriosuchus* or of any other important vertebrate were reported from the Aixheim region. This was to change beginning in the mid 1890's, when amateur scientists (e.g. from the Naturhistorischer Verein Spaichingen) prospected the quarries regularly and quarry owners apparently became aware that fossils represented a valuable side income. In the initial years, the SMNS acquired the first complete skull of *Mystriosuchus planirostris* including some postcrania, and two additional partial skeletons. In 1903, an excavation largely funded by the industrialist SIEGLIN yielded three more skulls and numerous postcrania (BERCKHEMER 1931, see list in Appendix C, 10.3) extending the SMNS collection of *Mystriosuchus*

planirostris specimens to the most important one. Only later, single specimens were purchased by other institutions (e.g. DREVERMANN 1918). The first new specimen (SMNS 9134) prompted Eberhard FRAAS (1896) to erect the new genus *Mystriosuchus* for the species *planirostris*, on the basis of skull physiognomy, but essentially because of differences in the tooth size and morphology from *Nicrosaurus kapffi*. MCGREGOR (1906) described the skull osteology of *Mystriosuchus planirostris*. This is still the most comprehensive account of the species available.

3.2.2 Systematic palaeontology

Synonymy:

Mystriosuchus planirostris (MEYER, 1863)
(Figs. 3.1 - 3.3)

? 1844 Zahn – MEYER: p. 44.

? 1847-55 Zahn – MEYER: p. 148, pl. 20 fig. 5.

? 1857 *Belodon Plieningeri* H. von Meyer – PLIENINGER [partim]: pp. 405, 435, 514, pl. 8 figs. 16, 32 [= *Mystriosuchus* sp.], non pp. 389-392 [= *Belodon plieningeri* MEYER, 1844 *nomen dubium*], non pp. 440, 446, pl. 8 fig. 1 [= *Nicrosaurus kapffi* (MEYER, 1860)], non pl. 8 figs. 3-6, 17-31, 36 [= Phytosauria indet.], non pl. 8 figs. 2, 7-15, 32-35, non pls. 9-13 [= *Plateosaurus engelhardti* MEYER, 1837], non p. 458 *Phytosaurus cylindricodon* JAEGER, 1828 [*nomen dubium*], non p. 458 *Phytosaurus cubicodon* JAEGER, 1828 [*nomen dubium*].

1862 Keupersaurier von Aixheim – ESER: p. 47.

1862 *Belodon planirostris* – MEYER: p. 335.

* 1863 *Belodon planirostris* – MEYER: p. 241, pl. 41 figs. 1-9, pl. 42 fig. 7, ? p. 244 "kleinerer Hautknochen", pl. 41 figs. 9-11 [= *Mystriosuchus* sp.].

1865 *Belodon planirostris* MEYER 1863 – MEYER: p. 106, 110. [1865b].

v 1865-66 *Phytosaurus cylindricodon* – QUENSTEDT [partim]: fig. 47, non p. 133, pl. 9 fig. 1 [= *Nicrosaurus kapffi* (MEYER, 1863)], non fig. 46 [= *Phytosaurus cubicodon* JAEGER, 1828, *nomen dubium*], non p. 135 "*Belodon plieningeri*" [= *Nicrosaurus* species B], non p. 134 "Schilder" [= *Paratypothorax andressi* LONG & BALLEW, 1985].

1872 *Phytosaurus planirostris* – SCHEMPP: p. 212.

1882-85 *Phytosaurus cylindricodon* Jaeger 1828 – QUENSTEDT [partim]: p. 17, fig. 58, non pl. 13 fig. 1 [= *Nicrosaurus kapffi* (MEYER, 1860)], non ? cf. *Belodon Kapffi* pl. 14 figs. 7-9 [= Phytosauria indet.], non fig. 57 [= *Phytosaurus cylindricodon* JAEGER, 1828, *nomen dubium*].

1987-90 *Belodon planirostris* Meyer – ZITTEL: p. 643.

v 1896 *Mystriosuchus planirostris* v. MEY. – E. FRAAS: p. 16, figs. 9-10, pl. 5 left.

1900 *Mystriosuchus planirostris* – E. FRAAS: p. 511.

1906 *Mystriosuchus planirostris* (H. von MEYER) – MCGREGOR: figs. 1-2, 5, 7, 9-11, pls. 6-7, pl. 11 figs. 48-49, ? fig. 8 [= *Mystriosuchus* sp.].

1907 *Belodon planirostris* MEYER – CUSHMAN: p. 272.

1907 *Belodon planirostris* Hermann von Meyer – ESER: p. 661.

1907-08 *Mystriosuchus planirostris* – HUENE: p. 396, fig. 349.

1907 *Mystriosuchus planirostris* – LEES: p. 122, 133, 134, tab. p. 147

1908 *Mystriosuchus* (*Belodon*) *planirostris* H. v. MEY. sp. – ENGEL: p. 169, 172, fig. p. 173.

1909 *Phytosaurus* (*Mystriosuchus*) *planirostris* H. v. MEYER sp. – HUENE: pp. 585, 592, fig. 2.

? 1910 *Mystriosuchus planirostris* H. v. MEY. – E. FRAAS: p. 23.

1910 *Mystriosuchus planirostris* v. MEYER – JAEKEL: p. 214, fig. 11.

1911 *Mystriosuchus planirostris* (H. von MEYER, 1863) – HUENE: p. 29, figs. 1 [cop. MCGREGOR 1906], 17, 18 [cop. HUENE 1909], 19, 21 [cop. HUENE 1907-08, newly lettered].

1913 *Mystriosuchus planirostris* – E. FRAAS: p. 1097. [1913a]

1913 *Mystriosuchus planirostris* – E. FRAAS: p. 275. [1913b].

v? 1913 *Mystriosuchus planirostris* M. – HUENE: figs. 1, 3, 5, 9.

1913 *Mystriosuchus planirostris* – MEHL: p. 188.

1914 *Mystriosuchus planirostris* – SCHMIDT: p. 31.

1914 *Mystriosuchus planirostris* (von MEYER) – WILLISTON: p. 185, figs. 92, 93 [cop. MCGREGOR 1906], 97.

1915 *Mystriosuchus planirostris* – HUENE: p. 491. [1915a].

1915 *Mystriosuchus* – HUENE: pp. 2, 16. [1915b]

1915 *Mystriosuchus planirostris* H. von MEYER – MEHL: pp. 129, 156, 162, fig. 6 [cop. MCGREGOR].

1916 *Mystriosuchus planirostris* – MEHL: p. 11.

1918 *Mystriosuchus planirostris* H. v. MEYER – DREVERMANN: p. 120, fig. p. 121 right.

1921 *Mystriosuchus planirostris* – HUENE: p. 564.

1922 *Mystriosuchus planirostris* – CASE: pp. 58, 69, fig. 23D-E [cop. MCGREGOR 1906].

1922 Mystriosuchus planirostris (H. von MEYER, 1863) – HUENE: pp. 60-65, 67, 72, 73, 75, 76, 78-79, 83-84, 86, 91, 96, 102, 103, 108, 109, 111, 113, 146, figs. 1-2, 34, 38, 42-47, 67-68.

1922 *Mystriosuchus* – MEHL: p. 146, 150.

1923 Phytosaurus Kapffii [sic] MEYER – ABEL [partim, "*Mystriosuchus planirostris*"]: p. 57, fig. 2, non fig. 1 [= *Mystriosuchus* species B], figs. 6-7 [*Nicrosaurus kapffi* (MEYER, 1860)].

1923 *Mystriosuchus planirostris* – HUENE: p. 369.

1928 *Mystriosuchus planirostris* – MEHL: pp. 157, 162, 166. [1928a].

1928 *Mystriosuchus planirostris* – MEHL: pp. 7, 11. [1928b].

1928 *Mystriosuchus planirostris* H. v. MEYER – SCHMIDT: p. 417, fig. 1171 [modified after FRAAS 1896].

1929 *Mystriosuchus planirostris* – CASE: pp. 24, 25, 43, ? p. 50 [ilium, = Phytosauria indet.].

1929 *Mystriosuchus* – STOLL [partim]: p. 48 [includes *Mystriosuchus* species B].

1930 *Mystriosuchus planirostris* (H. von MEYER, 1863) – CAMP: p. 141, fig. 6, tab. 6, pp. 63, 64, 66, 67 [cervical vertebrae], ? pp 68-89 other postcrania including pp. 72 scapula, 76 ilium [fig. MEYER (1865b: pl. 29 fig. 1)], 85 fibula [fig. HUENE (1922: fig. 53)], 86 metacarpal [fig. HUENE (1922: fig. 44)] [= all Phytosauria indet.].

1931 *Mystriosuchus planirostris* (Hermann von MEYER) – BERCKHEMER: pp. 4, 8, figs. 1, 2 [cop. ABEL 1923].

1932 *Mystriosuchus planirostris* – CASE: p. 74. [1932b].

1933 *Mystriosuchus planirostris* H. v. Meyer sp. – KUHN: p. 19.

1934 *Mystriosuchus planirostris* – KUHN: p. I.

? 1936 *Mystriosuchus planirostris* H. v. M. – KUHN: p. 86 [= Phytosauria indet.].

non 1938 *Mystriosuchus* – BERCKHEMER: p. 194, figs. 44, 52 [= Phytosauridae indet.].

1947 *Mystriosuchus planirostris* – COLBERT: p. 80, fig. 12 top, tabs. 1, 5-6.

1955 *Mystriosuchus planirostris* (Meyer) – HOFSTETTER: p. 690, fig. 11D [cop. MCGREGOR 1906].

1956 *Mystriosuchus planirostris* – HUENE: p. 463, fig. 496c [cop. HUENE 1911].

1962 *Mystriosuchus planirostris* MEYER, 1863 – GREGORY: p. 675, figs. 1C, 3D [both cops. MCGREGOR 1906], 4, 5B [cop. MCGREGOR 1906], tabs. 1-4. [1962a].

1962 *Mystriosuchus planirostris* – GREGORY: pp. 10, 11, 12, 17. [1962b].

1963 *Belodon planirostris* – WESTPHAL: p. 121, fig. 5 centre. [1963a].

1963 *Belodon planirostris* H. v. MEYER 1863 – WESTPHAL: p. 165, fig. 1 centre. [1963b].

1963 *Belodon planirostris* H. v. Meyer 1863 – WESTPHAL: p. 22. [1963c].

1968 *Mystriosuchus* – WALKER: p. 12.

1968 *Belodon* (*Mystriosuchus*) *planirostris* H. v. MEYER – KUHN: p. 75, figs. 36, 1-2.

1969 *Mystriosuchus planirostris* MEYER 1863 – GREGORY [partim]: p. 42, fig. 2, non p. 46 "großer Schädel" [= *Mystriosuchus* species B].

1969 *Mystriosuchus planirostris* (MEYER 1863) – GREGORY & WESTPHAL [partim]: pp. 1297, 1297, non p. 1296 "v. Huene (1911, pls. 12-14)" [= *Mystriosuchus* species B].

1970 *Mystriosuchus planirostris* – WESTPHAL: fig. 1i.

1971 *Mystriosuchus planirostris* MEYER 1863 – KUHN [partim]: p. 14, fig. 24(2) [cop. HUENE 1956], fig. 24(5) [cop. WESTPHAL 1970], fig. 25 right half fig. 1 [cop. GREGORY 1969], non p. 14, figs 24(3), 25(2-3) [= *Mystriosuchus* species B].

1973 *Mystriosuchus planirostris* H. v. M. – BRENNER: p. 171.

1976 *Mystriosuchus planirostris* (H. von MEYER, 1863) – WESTPHAL: p. 113, figs. 1b, 4k, 10, 13.

1978 *Mystriosuchus planirostris* (MEYER), 1863 – CHATTERJEE: p. 115, fig. 16a [cop. MCGREGOR 1906], fig. 18, tab. 3.

1978 *Mystriosuchus planirostris* – DUTUIT: p. 87.

1985 *Mystriosuchus planirostris* (H. v. MEYER) – MÜLLER: p. 317, figs. 382-383 [cops. MCGREGOR 1906].

1986 *Mystriosuchus* – ZIEGLER: p. 133, fig. 155.

1987 *Mystriosuchus* sp.– PINNA: p. 67, fig. p. 70.

1988 *Mystriosuchus* – ZIEGLER: p. 19, fig. 19.

1989 *Pseudopalatus* (*Mystriosuchus*) *planirostris* (MEYER, 1863) – BALLEW: p. 332.

1989 *Mystriosuchus planirostris* (MEYER, 1863) – HUNT & LUCAS: p. 343, fig. 1. [1989b].

1989 *Mystriosuchus* – PARRISH: p. 363.

? 1989 *Mystriosuchus planirostris* Meyer – WILD: p. 15.

? 1991 *Mystriosuchus planirostris* – WILD: p. 60.

non 1992 *Mystriosuchus planirostris* – SERENO & WILD: p. 436.

1993 *Mystriosuchus* – BENTON & WILD: p. 37.

? 1993 *Mystriosuchus planirostris* – BUFFETAUT: p. 42.

1993 *Mystriosuchus planirostris* – BUFFETAUT: p. 42, fig. 4.
1994 *Mystriosuchus planirostris* – HUNT: 30A.
1995 *Mystriosuchus planirostris* – HUNGERBÜHLER: p. 67, figs. 1a, 2.
1995 *Mystriosuchus planirostris* (MEYER, 1863) – LONG & MURRY: p. 38.
1996 *Mystriosuchus* – GALTON & WALKER: p. 733.
1997 *Mystriosuchus planirostris* – WITMER: pp. 12, 33, 48.
1998 *Mystriosuchus planirostris* – RENESTO & PAGANONI: p. 119, fig. 1, pl. 1.

Lectotype (designated in HUNT & LUCAS 1989b):

MCZ 1018, right preorbital part of a skull lacking most of the rostrum (MEYER 1863: pl. 41 figs. 1-3; HUNT & LUCAS 1989b: fig. 1).

Paralectotypes:

MCZ 1019A: rostral fragment (MEYER 1863: pl. 41 figs. 4-6)
MCZ 1019B: rostral fragment including one tooth (MEYER 1863: pl. 41 figs. 7-9)
MCZ 1019C: rostral fragment (MEYER 1863: 243)
MCZ 1022A: dorsal skull fragment (frontal or parietal: MEYER 1863: 244)
(?) MCZ 1022B: partial centrum of a caudal vertebra, not mentioned in the original description

Remark: The types were recently rediscovered at Harvard University by HUNT & LUCAS (1989b), who designated the lectotype. The majority of the former ESER collection including the type series of *Mystriosuchus planirostris* was purchased by the Boston Society of Natural History in the early 1870s (CUSHMAN 1907; ESER 1907; BERCKHEMER 1931). This explains the acronym BSNH on some specimen labels that puzzled previous workers (HUNT & LUCAS 1989b). According to MEYER (1863: 243), the type series represents one individual.

Type locality: Neuhaus near Aixheim, southern Württemberg (ESER 1907; Fig. 1.1).

Type horizon: middle Stubensandstein, sandstone subunit sc3 (Appendix C, 10.1).

Referred specimens:

(1) Skulls, skull fragments and articulated postcrania

SMNS 9134: anterior part of the snout (the remainder of the skull has been lost in WW II), a ceratohyal, the articulated cervical vertebrae 1 to 5 with parts of the cervical ribs, the complete throat shield, 1 osteoderm (FRAAS 1896: figs. 9-10, pl. 5 fig. 2;

MCGREGOR 1906: pls. 6-7; Fig. 3.1). SMNS 9134 is the essential specimen described by MCGREGOR (1906) and the basis of his skull reconstruction. Additionally collected were a coracoid, a radius, and numerous ribs (FRAAS 1896); these could not be identified in the SMNS collection. Aixheim region, exact provenance unknown. Acquired from the Naturhistorischer Verein Spaichingen, 1896.

SMNS 10260: articulated partial skeleton consisting of the skull with the mandible in occlusion, but lacking the rostrum and the symphyseal part, 11 presacral vertebrae, the shoulder girdle, numerous ribs and gastrals, the left forelimb lacking all phalanges, and 13 paramedian osteoderms (MCGREGOR: fig. 10, pl. 11 fig. 49; HUENE 1922: figs. 21, 34a-b, 42-47, 67-68; this study, Fig. 3.3C, D). Part of the material described by MCGREGOR (1906). The axial skeleton except the dermal scutes is presently on display. Quarry BRAUN, (?) Neuhaus, 1899.

SMNS 11126(1): left half of a postorbital skull (HUENE 1911: fig. 20). The specimen was severely damaged by fire in 1944: the occipital condyle, the basipterygoid process, the parasphenoid, and the area in front of the posterior nasal rim are lost. The region around the prootic foramen and the exit of nerve VII is largely flaked off. Many of the details figured by HUENE are now obscured by scorching. Quarry "Wannengrund" to the west of Aixheim. Excavation SIEGLIN 1903.

SMNS 13007: complete skull with the mandible in occlusion (on display mounted on the postcrania of SMNS 10260), the articulated cervical vertebrae 1 to 7 with the neural arches and ribs, the complete throat shield, and the medial parts of the clavicles (HUENE 1922: fig. 2a-c). Quarry JETTER, Neuhaus, 1912.

SMNS 13240: complete skull with the mandible in occlusion. Quarry JETTER, Neuhaus, 1913.

SMNS uncat. no. 184: largely undistorted skull lacking most of the rostrum and the symphyseal part (Fig. 3.3A, B). The specimen shows a highly abraded palate that is the basis of MCGREGOR's (1906) description. Aixheim region, exact provenance unknown.

SMNS uncat. no. 185: skull with the mandible in occlusion lacking most of the rostrum, almost free of matrix, strongly distorted obliquely. Aixheim region, exact provenance unknown.

SMNS uncat. no. 397: skull with the mandible in occlusion but, lacking most of the rostrum and the symphysis. Presently on loan to Heimatmuseum Trossingen. Aixheim region, exact provenance unknown.

SMNS uncat. no. 205: steinkern of a skull, recovered from the destroyed museum building in 1944. Probably Aixheim region.

GPIT 249/002: right side of a rostrum (HUENE 1909: fig. 2). Aixheim region, exact provenance unknown.

HMB MB.I.008.05: complete skull lacking the mandible. Aixheim region, exact provenance unknown.

FSF unnumb.: complete skull lacking the mandible (DREVERMANN 1918: fig. 2). Aixheim region, exact provenance unknown. Acquired in 1913.

AMNH 10644: right half of a skull, *fide* WITMER (1997).

GPIT 2074.000: basioccipital and basisphenoid, partly abraded. Quarry "Untere Mühle", Trossingen.

GPIT 2149.002: fragment of a right cheek including the quadratojugal process of the squamosal, the quadratojugal, and the posterior part of the jugal). Quarry "Untere Mühle", Trossingen.

GPIT 2149.003: anterior part of a left jugal. Quarry "Untere Mühle", Trossingen.

GPIT 2150.000: posteroventral part of a right quadrate. Quarry "Untere Mühle", Trossingen.

MBSN 2: complete skull lacking the mandible, badly crushed (PINNA 1987: fig. p. 70; RENESTO & PAGANONI 1998: pl. 1), *fide* RENESTO & PAGANONI (1998). Endenna, Lombardy, Italy.

NMW unnumb.: complete skull lacking the mandible (BUFFETAUT 1993: fig. 4), *fide* BUFFETAUT (1993). Totes Gebirge, Steiermark (Styria), Austria.

(2) Mandibles

SMNS uncat. no. 180: complete mandible without teeth. Weißer Steinbruch, Pfaffenhofen.

SMNS uncat. no. 183: right mandibular ramus. Quarry Wannengrund, Aixheim. Excavation SIEGLIN 1903.

There are a great number of additional partial snouts and mandibular fragments kept in the SMNS and GPIT, the general morphology of which (slenderness, spacing of the alveoli) and the provenance do not contradict a referral to *Mystriosuchus planirostris*. Particularly intriguing are three specimens:

SMNS 12671: tip of both premaxillae with well preserved teeth, strongly laterally compressed (BERCKHEMER 1931: fig. 52). Quarry Weißer Steinbruch, Pfaffenhofen.

SMNS uncat. no. 2: anterior snout fragment to the anterior part of the maxillae with a flat rectangular cross-section (MEYER 1861: p. 280f). The specimen lacks the gradual slope toward the naris seen in *Nicrosaurus* species B, but has a broad interpremaxillary groove unlike *Mystriosuchus*. Heslach.

GPIT 2088.002: three fragments of a right anterior premaxilla. The premaxillae show a small premaxillary crest on the extremity of the snout. Aixheim region, exact provenance unknown.

These specimens are important because a secure identification as *Mystriosuchus planirostris* could provide information on the morphology of the fangs (SMNS 12671) and would represent the first evidence for a premaxillary crest (GPIT 2088.002) in this species. Furthermore, SMNS uncat. no. 2 would demonstrate the presence of *Mystriosuchus planirostris* in the Heslach phytosaur fauna. However, not a single specimen is complete enough to determine the ratio of the mandibular to the symphyseal length, and the characteristic teeth of *Mystriosuchus planirostris* are not preserved. SMNS 12671 and GPIT 2088.002 cannot be distinguished from *Nicrosaurus* species B by means of diagnostic characters, and the evidence is ambiguous in SMNS uncat. no. 2. Hence, all three specimens and all the additional material mentioned must be considered even generically indeterminable.

Summary description (suggested diagnostic characters excluded): medium-sized (skull length up to 800 mm), slender-snouted species of *Mystriosuchus*; snout greatly elongated; snout sculptured with deep longitudinal grooves; anterior part of the naris faces anterodorsally; postorbital part of the skull high and anteroposteriorly abbreviated; parietal foramen may be present; posterior process of the squamosal present, but very short; extremity of the squamosal narrows to a more pointed tip than in *Mystriosuchus* species B, sometimes distinctively knob-like because of a constriction; furrow on the posterior face of the squamosal; parietal process of the squamosal does not meet the supraoccipital; supraoccipital excluded from the posttemporal fenestra; ventral opisthotic ridge well demarcated, often with a ventral prong; tympanic fossa wide and not well-demarcated from paroccipital process; base of the pterygoid process of the basisphenoid long, slender, and round in cross-section; basisphenoid strongly constricted between tubera and pterygoid processes; basal tubera oval and well separated; one small, oval suborbital opening; ventral rim of the jugal-quadratojugal bar sharp; dentition bipartite, comprising predominantly slender, acarinate to faintly monocarinate, basally fluted teeth, but small bicarinate teeth occur regularly in the posteriormost positions; symphysis equals c. 60% of the total length of the mandible; suprafenestral process of the dentary borders the external mandibular fenestra; weak lateral crest of the surangular; triangular postglenoidal facet high and narrow; longer retroarticular process than *Nicrosaurus*.

Suggested diagnostic characters (see discussion in part 3.2.3.1): rostrum greatly elongated; steeply sloping prenarial region; perpendicular rim of the internasal septum; naris separated into a dorsally and an anteriorly facing part; raised posterolateral borders of the supratemporal fenestra; depression of the parieto-squamosal bar exceeds 30% of the skull height.

Distribution: central Europe: in southern Württemberg in the region around Trossingen and Aixheim, in northern Württemberg at Pfaffenhofen (Fig. 1.1); in the Tethydian realm: Styria (Austria), Lombardy (northern Italy).

Stratigraphic range: in Germany Upper Triassic, Keuper succession, Middle Keuper, Stubensandstein, restricted to the middle Stubensandstein.

Age: Middle (?) Norian, Late Triassic.

3.2.2 Description

The skull anatomy of *Mystriosuchus planirostris* was described in detail by MCGREGOR (1906), based on the specimens SMNS 9134, SMNS uncat. no. 184, and two unidentified skulls from the same collection (among them most probably SMNS 10260). MCGREGOR also presented a description of the postcrania found in articulation with SMNS 9134 and SMNS 10260. HUENE (1909) identified the septomaxilla and presented a description of the internal aspect of the braincase in 1911. Later, HUENE (1922) provided additional information on the axial skeleton and the fore limb based on the articulated specimens. Since MCGREGOR collected the data for his monograph in 1900, considerably more cranial material has accumulated in various institutions. However, all of these specimens (as well as the identifiable skulls used by MCGREGOR) are only prepared from the dorsal and lateral sides. To obtain more precise anatomical information on the anatomy of the palate and the external aspects of the braincase which is still wanting would have required substantial repreparation, with no guarantee of sufficiently well preserved features. Also, a full redescription of the skull, or a comprehensive variational study of the cranial characters in *Mystriosuchus planirostris*, should include the new specimens from Austria and Italy, which have been only briefly reported so far (BUFFETAUT 1993; PINNA 1987; RENESTO & PAGANONI 1998). Consequently, this section comprises a redescription of the important external aspects of the narial, temporal, and occipital regions of *Mystriosuchus planirostris* only. Some additional characters are noted that have bearing on the taxonomic status of the species.

Sculpture. The skull roof and the narial region of *Mystriosuchus* is deeply sculptured. The pits are larger and much deeper than in both *Nicrosaurus* species and for this reason dominate the overall appearance of the sculpture. The concavities tend to

anastomose and are then surrounded by sharper, meandering and multifurcating ridges. The extraordinary depth of the pits leads to a raised rim of the borders of the skull roof, which is particularly well developed around the orbit and along the anterior transverse rim of the supratemporal fenestra.

The anterodorsal corner of the orbit is conspicuously raised in *Mystriosuchus planirostris* (e.g. SMNS 10260, SMNS uncat. no. 185). The orbital rim thus marks a sharply outlined crescentic depression just in front of the orbit, which is much deeper than the surrounding concave ornamentation of the skull surface. The structure is named preorbital depression, and represents a synapomorphy shared by both *Mystriosuchus* species.

Narial region. *Mystriosuchus planirostris* shows a consistently elevated narial crater (but see part 2.3.3.1). By contrast to a statement in BALLEW (1989), the nasal openings are not elevated above the skull roof (HUNT & LUCAS 1989b). The skull roof is not preserved in the lectotype of *Mystriosuchus planirostris*, but the region between orbits and nares is clearly ascending in posterior direction (e.g. MEYER 1863: pl. 41 fig. 2, pl. 42 fig. 7). In all other specimen of *Mystriosuchus* regardless of their specific assignment, the external nasal openings are consistently placed below or terminate at level of the skull roof at best. A very prominent narial wing is developed, separating the naris into a posterior part facing dorsally, and an anterior section that opens anterodorsally to anteriorly by means of a broad groove along the maxilla-septomaxilla contact. The internasal septum thus projects more prominently above the narial rim in the anterior part of the nares as in the specimens of *Nicrosaurus* species B showing the same condition. HUNT & LUCAS (1989b) were the first to note that the septum terminates in a vertical anterior edge, set at a right angle with the horizontal dorsal rim (MCZ 1018, SMNS 10260, SMNS 13240, HMB MB.I.008.05). The prominent angular anterior part is broken off in the other specimens, and for this reason the character has probably been overlooked in previous descriptions.

Skull roof. The postorbito-squamosal bar of *Mystriosuchus planirostris* is similar to GPIT 261/001 described in subsection 3.3.2. In *Mystriosuchus planirostris*, the lateral ridge on the postorbito-squamosal bar is similarly strongly developed and overhangs the sides of the skull. It is associated with a narrow groove underneath, which leads into a foramen in the postorbital close above the anterodorsal corner of the infratemporal fenestra. This groove is bordered ventrally by another, fainter ridge, which separates the groove from the smooth, vertical area that leads into the infratemporal fenestra. It is likely, that in analogy with modern crocodiles the second faint ridge served as an

insertion for a membrane spanning the large opening. The same condition applies to *Mystriosuchus* species B.

There is one specimen, the comparatively small skull SMNS 13240, showing a parietal foramen located on the suture of both parietals level with the anterior rim of the supratemporal fenestrae. The specimen lends further support to the suggestion, that the persistence of this structure is an ontogenetically variable feature and less uncommon in phytosaurs than thought previously.

Temporal region. An important difference between *Mystriosuchus*, and *Nicrosaurus* representing in fact all other taxa with depressed parieto-squamosal bars, is developed on the ventral surface of the posterior process. In *Nicrosaurus*, the parieto-squamosal bar contacts the ventral surface of the squamosal tangentially and continues as a straight ridge as far as to the extremity of the squamosal (Fig. 2.8). The parieto-squamosal bar in *Mystriosuchus* meets the squamosal almost perpendicular at a point far more ventrally than in *Nicrosaurus*, and merges to the ventral surface (because of the inclined squamosal, the ventral surface is actually facing almost medially), being upturned in a steeply curved arc (Fig. 3.3A, C). For this reason, the area corresponding to the dorsal recess of *Nicrosaurus* covers in *Mystriosuchus* almost the whole ventral surface of the squamosal. The ridge of the parieto-squamosal bar is shorter, arched (Fig. 3.3C), and because of its peripheral position the squamosals of *Mystriosuchus* appear to be undivided into dorsal and ventral sulcus. Secondly, the well marked ventral sulcus of *Nicrosaurus* is reduced to a narrow groove in *Mystriosuchus*, because the parieto-squamosal bar is intimately applied to the paroccipital process. Furthermore, the triangular recess of *Mystriosuchus* is greatly enlarged (Fig. 3.3A, C). HUENE (1922: 87) was the first author to note this distinction.

In contrast to *Mystriosuchus* species B, *Mystriosuchus planirostris* has a posterior process of the squamosal, although the process is short and overhangs for about 10 mm the paroccipital processes of both the opisthotic and the squamosal, and also the posterior extremity of the quadrate. The medial and lateral rims of the horizontal squamosal plane converge posteriorly. Especially, there is a consistent and distinct bulge inward of the lateral rim of the supratemporal fenestra at level with the posterior edge of the supraoccipital shelf (Fig. 3.3B, D). This results in a pointed posterior process, rather than the blunt extremity of the squamosal seen in *Mystriosuchus* species B. Nevertheless, *Mystriosuchus planirostris* shows considerable variation regarding the shape of the posterior process. The dorsal surface of the extremity is usually narrow to taper in a prong (Fig. 3.3D), but may remain comparatively broad in some specimens (SMNS uncat. no. 184: Fig. 3.3B, GPIT 2149.001, GPIT 2103.005). A distinct "knob" may be developed (SMNS 13240, GPIT 2221.000, GPIT 2112.000) because of an elongation of

the tip and a rapidly bulging medial rim of the squamosal, which can lead to a constriction just in front of the tip (Fig. 3.3B). A similar squamosal knob was suggested as a synapomorphy of the clade *Pseudopalatus pristinus* + *Arribasuchus buceros* (BALLEW 1989: character 50; however, her cladogram reproduced here in Figure 5.1 shows this clade to be paraphyletic), but the character actually occurs in a few specimens of *Mystriosuchus planirostris* as well. In occipital view, the descending part of the squamosal between the tip of posterior process and the triangular recess above the paroccipital process varies from being narrow and round (SMNS 10260: Fig. 3.3C, SMNS 13240, SMNS uncat. no. 185, GPIT 2103.005) to broad and concave. In SMNS uncat. no. 184, the concavity is developed as a marked vertical furrow (Fig. 3.3A). This seems to coincide with the knob on the posterior process overhanging the furrow. In conclusion, a distinction between the species of *Mystriosuchus* based on squamosal morphology alone seems impossible because of the variability seen in *Mystriosuchus planirostris*. However, a distinct and sharp knob at the extremity of the squamosal may be present only in *Mystriosuchus planirostris* so far.

Although there is a wealth of morphological data available from the other skulls, only the parietal-supraoccipital complex of SMNS 13007 is sufficiently well preserved to exhibit the entirety of the osteological configuration (Fig. 3.2). The squamosal processes of the parietals form a tall and narrow, pillar-like structure. This consists of a marked horizontal ledge of the parietals roofing over the supraoccipital shelf, from which two thin and sharp laminae descend vertically, framing the supraoccipital shelf. Usually, there is a slight transverse constriction of both descending laminae at the mid-height of the parietal-supraoccipital complex. Almost the entire lamina is formed by the squamosal process of the parietal. There is no evidence in SMNS 13007 and the other specimens for a supernumerary occipital ossification as in *Mystriosuchus* species B GPIT 261/001. The specimen also clearly shows no extended lamina sheathing the supraoccipital shelf, but an essentially straight suture with the supraoccipital that confines the process to the vertical descending lamina. The parieto-squamosal bar then turns into a transverse and thin, horizontal bar, which is closely appressed onto the paroccipital process (Fig. 3.3A, C). The parietal interdigitates with the parietal process of the squamosal, reaching as a narrow tongue-like projection to about the midline of the supratemporal fenestra (SMNS 13007: Fig. 3.2, SMNS uncat. no. 185). In several specimens, the flat surface of the lateral part of the parieto-squamosal bar bears two posterolaterally running rugose grooves, which are readily confused with sutures (e.g. SMNS 10260), but judging by SMNS 13007 actually represent ornamentation on the parietal process of the squamosal. The process merges with the paroccipital process over a comparatively long distance medial to the posttemporal fenestra. A suture to the opisthotic is not discernible, but it is likely from

SMNS 13007 (left-hand side), that the squamosal does not touch the supraoccipital (Fig. 3.2).

The minimum depression of the parieto-squamosal bar below the skull table is always more than 30% of the total height of the skull (Appendix B, Tab. B4). The supraoccipital shelf is thus high and narrow, but anteroposteriorly abbreviated. SMNS 13007 shows no indication of an unpaired postparietal (Fig. 3.2). In MCGREGOR's (1906) reconstruction of the occipital aspect, probably based on SMNS 9134, the supraoccipital is high and narrow, and does not extend laterally to the posttemporal fenestrae. Such a condition is corroborated by SMNS 13007.

In two specimens (SMNS 10240, SMNS 13007: Fig. 3.2), the exoccipital-opisthotic suture persists externally over a short distance. The posteromedian ridge of the paroccipital process is usually weak and more readily described as a rounded posteromedian face of the paroccipital process, but may occasionally be a prominent and sharp edge (HMB MB.I.008.05). The ventral opisthotic ridge is always well demarcated from the medial part of the process, and its medial edge forms in some specimens a ventrally directed prong (Fig. 3.3C). In contrast to *Nicrosaurus*, the lateral part of the paroccipital process is of roughly rectangular shape. Its posterior surface is not flat and vertically oriented, but much more convex and largely facing posterodorsally. This results in a narrow fissure (the equivalent of the ventral sulcus described in *Nicrosaurus*, Fig. 2.8) leading into the posttemporal fenestra (Fig. 3.3A, C).

The posttemporal fenestra is greatly reduced in width and height, but in *Mystriosuchus planirostris* still retains its plesiomorphic oval shape. It differs from other phytosaurs in being situated below the central third of the supratemporal fenestra, rather than the medial half, and in being hidden in the fissure between parieto-squamosal bar and paroccipital process.

Basicranium. The basal tubera are best preserved and accessible in SMNS uncat. no. 184 and GPIT 2074.000. The parts of the tubera bearing the rugosities for muscle attachments are suboval in shape with a more pointed side facing medially, and comparatively small. Both tubera are widely separated by a broad (more than one tuberal width), concave and rugose area (also SMNS uncat. no. 185). The area of the basisphenoid contributing to the tuberal surface equals that of the basioccipital; the suture is marked by a transverse ridge on the tubera that continues onto the intertuberal area. The tubera as well as the tuberal surfaces face exactly ventrolaterally, rather than showing a posterior orientation as in *Nicrosaurus*. The foramen of the hypoglossal nerve XII is widely separated from the jugular foramen (HUENE 1911: fig. 20).

Dentition. It is frequently stated that *Mystriosuchus planirostris* is the only phytosaur with a homodont dentition (MCGREGOR 1906; WESTPHAL 1963b; CHATTERJEE 1978; BALLEW 1989; LONG & MURRY 1995). This is incorrect. The nature of the dentition in *Mystriosuchus planirostris* is actually weakly, but clearly bipartite heterodont. The majority of teeth correspond to the morphology outlined by MCGREGOR (1906) in being high and slender, and in showing a round to oval cross-section and a base of a tooth crown prominently fluted by widely spaced ridges. A faint, unserrated carina is frequently developed on the distal face of the crown. While being uniform in the more anterior section of the dentition, the height of the crowns decreases rapidly in the posteriormost five or six positions of the maxilla. Simultaneously, the tooth morphology becomes bicarinate and serrated, flattened lingually, and markedly curved inward (SMNS 10260, SMNS 13240, SMNS uncat. no. 185). Posteriormost maxillary teeth resemble those of *Nicrosaurus* species B, but differ in being smaller, stouter, and having no expanded blades and a rather blunt, ventrally and lingually pointing apex. The spacing of the teeth diminishes gradually from very wide anteriorly (four to three alveoli diameters) to rather close (half an alveolus diameter) in the posteriormost positions. In the anterior part of snout, the base of a premaxilla tooth is strongly curved lateroventrally, and snout and teeth form a hemicylindrical cage. In occlusion, each tooth in the lower jaw touches the distal face of its antagonist, leaving a wide interdental gap to the following tooth pair (SMNS 9134).

3.2.3 The diagnostic characters of *Mystriosuchus planirostris*

In this section, the characters identified as diagnostic for *Mystriosuchus planirostris*, and characters distinguishing this species from *Mystriosuchus* species B, are listed and discussed. For convenience, the complementary state of each character state pair is given in parenthesis.

3.2.3.1 Diagnostic characters

(1) strongly elongated rostrum: ratio of the prenarial to narial + postnarial skull length exceeds 2.6 (GREGORY 1962a), snout length equals four times the orbital + postorbital skull length; [ratio of the prenarial to narial + postnarial skull length considerably less than 2.6].

The rostrum (prenarial part of the skull) of *Mystriosuchus planirostris* is by far the longest among phytosaurs. *Ebrachosuchus neukami* is the only taxon with a comparable snout length, although the prenarial to narial + postnarial length is far less than in *Mystriosuchus planirostris* because of the more anterior position of the nares in this primitive taxon. The length of the snout (preorbital part of the skull) compared to the orbital + postorbital part is in both species almost identical (*Mystriosuchus planirostris*: 3.9 - 4.1; *Ebrachosuchus*: 3.8).

(2) steeply sloping snout profile; [gently sloping snout profile].

A broadly similar character state is present in *Pseudopalatus pristinus*, but in some specimens, there is a large prenarial hump extending for some distance in front of the external nasal openings. *Mystriosuchus planirostris* shows a steep descent of the snout profile starting directly in front of the nares. Furthermore, the slope of the prenarial surface in *Pseudopalatus pristinus* is not as steep as in *Mystriosuchus* planirostris, and the slope is far more gently in any other taxon with slender, uncrested rostrum.

(3) protruding anterior part of the internasal septum with perpendicular anterior rim (HUNT & LUCAS 1989b); [internasal septum with rounded, sloping anterior rim].

In other phytosaurs with anteriorly visible internasal septa (e.g. *Nicrosaurus* species B) the anterior rim is not angular but gently sloping. The character state "perpendicular anterior rim" cannot be demonstrated for *Mystriosuchus* species B for preservational reasons and the pathologic condition of the nasal opening in GPIT 261/001. The perpendicular rim of the internasal septum is tentatively regarded as diagnostic for *Mystriosuchus planirostris* only.

(4) external nasal opening subdivided into a posterior section facing dorsally, and a strongly inclined anterior section that opens anteriorly; [rim of the external nasal opening straight or undulating].

(5) raised border of supratemporal fenestra extends posteriorly along medial rim of squamosal; [rim of supratemporal fenestra not raised or confined to the anterior border].

(6) depression of the parieto-squamosal bar exceeds 30% of the skull height; [depression of the parieto-squamosal bar maximal 30%].

This is the maximum depression of the parieto-squamosal bar seen in a phytosaur, and *Mystriosuchus planirostris* is thus the most derived taxon in this respect.

3.2.3.2 Characters distinguishing *Mystriosuchus planirostris* from *Mystriosuchus* species B

The characters other than the diagnostic ones that are different from *Mystriosuchus* species B are listed as the complementary character states (1) - (13) in part 3.3.4.2.

3.2.3.3. Rejected diagnostic characters for *Mystriosuchus planirostris*

With the recognition of status of *Mystriosuchus* species B as a separate species of *Mystriosuchus*, the character (3) listed in part 3.1.2.1, deep sculpture of the skull roof and the narial region, that has been suggested diagnostic for *Mystriosuchus planirostris* previously, actually becomes diagnostic for the genus *Mystriosuchus*. The character (i) - (v), (vii), and (xi) - (xiii) discussed in part 3.1.2.2 have been previously established as diagnostic based on *Mystriosuchus planirostris* in a then monotypic *Mystriosuchus*, and must be rejected as diagnostic for this species because of the reasons given in that section.

Section 3.3
Mystriosuchus species B

The skull GPIT 261/001 was long regarded as the typical representative of "*Belodon plieningeri*". The consequences for this taxon, in the present study named *Nicrosaurus* species B, are discussed in subsection 2.3.1. GREGORY (1962a, 1969) and GREGORY & WESTPHAL (1969) were the first to realise that the specimen should be referred to the genus *Mystriosuchus* following the definition of GREGORY 1962a, *non* HUENE 1911. However, they interpreted GPIT 261/001 as a somewhat aberrant *Mystriosuchus planirostris*, and the specific identification was by no means fully established in the literature (e.g. WESTPHAL 1963b, 1976). HUNT & LUCAS (1989b), followed by LONG & MURRY (1995), suggested that the Trossingen skull represented a species different from the type species of *Mystriosuchus*, and in both papers a total number of 11 characters were presented in support of a specific segregation. However, none of these features is a clearly autapomorphic character state. It was thus desirable to reinvestigate GPIT 261/001 in order to establish its previously suggested specific identity, to review the criteria distinguishing the taxon from *Mystriosuchus planirostris*, and to define the new species by autapomorphies.

3.3.1 Systematic palaeontology

Synonymy:

Mystriosuchus species B
(Figs. 3.4 - 3.10)

v 1909 *Phytosaurus Plieningeri* H. v. MEYER sp. – HUENE [partim]: p. 583, figs. 1, 5-7, non pp. 586, 592 [= *Nicrosaurus* species B].

v 1911 *Mystriosuchus Plieningeri* H. v. MEYER sp. – HUENE [partim]: pp. 68, 91, pls. 12-14, pl. 17 fig. 7, figs. 2-9, non p. 88, non pl. 15, non figs. 10-11 [= *Nicrosaurus* species B].

1915 *Mystriosuchus plieningeri* – HUENE [partim]: p. 491 [includes *Nicrosaurus* species B]. [1915b].

1915 *Belodon* (*Mystriosuchus*) *plieningeri* H. von Meyer sp. 1842 – MEHL [partim]: pp. 162, 144, 147, non p. 150 [= *Nicrosaurus* species B].

1916 *Belodon* (*Mystriosuchus*) *pleiningeri* [sic]– MEHL : pp. 13, 14.

1922 *Mystriosuchus pleiningeri* [sic] – CASE: pp. 59, 68.

1922 *Mystriosuchus Plieningeri* H. v. MEYER – HUENE [partim]: pp. 60, 67, 86, 99, 100, non p. 60 "Heslach und Kaltental", p. 60 "Pfaffenhofen am Stromberg", p. 88 "Sutur des Angulare" [= *Nicrosaurus* species B], non p. 146 [= *Mystriosuchus ingens* E. FRAAS, 1896, *nomen nudum*].

1923 *Phytosaurus Kapffii* [sic] MEYER – ABEL [partim, "*Mystriosuchus Plieningeri*" H. v. MEY.]: pp. 26, 30, 31, fig. 1 [cop. HUENE 1911], non pp. 44, 45 [= *Nicrosaurus* species B].

1923 *Mystriosuchus Plieningeri* – HUENE: p. 369.

1923 *Mystriosuchus Plieningeri* – MOODIE: p. 121, pl. 26 fig. c [cop. HUENE 1911]. [reprinted 1980]

1928 *Mystriosuchus Plieningeri* H. v. MEYER sp. – SCHMIDT [partim]: p. 418, figs. 1172a, 1172b [cops. HUENE 1911], non fig. 1172a mandible [cop. HUENE 1911], non p. 418 "Symphyse des Unterkiefers" [= *Nicrosaurus* species B].

1930 *Mystriosuchus plieningeri* – CAMP [partim]: fig. 6 ["33.3%"], non fig. 6 ["37.5%", = *Nicrosaurus* species B].

1931 *Belodon Plieningeri* – BERCKHEMER: p. 6.

1933 *Mystriosuchus plieningeri* v. H. – SEEMANN: p. 134.

1933 *Mystriosuchus plieningeri* H. v. Meyer sp. – KUHN [partim]: p. 20.

1934 *Mystriosuchus pleiningeri* [sic] – CASE & WHITE: p. 137.

1935 *Mystriosuchus plieningeri* Meyer – ABEL: p. 570, fig. 473A [cop. HUENE 1911].

1936 *Mystriosuchus plieningeri* – KUHN: p. 76.

1937 *Mystriosuchus* – KUHN: p. 82, fig. 65 [cop. HUENE 1911, newly lettered].

1941 *Mystriosuchus* – KUHN: p. 49, fig. 49 [cop. HUENE 1911].

1954 *Mystriosuchus plieningeri* – HELLER: p. 10.

1956 *Mystriosuchus* – HUENE: fig. 496a-b [cops. HUENE 1911, newly lettered].

1958 *Mystriosuchus* – KUHN: fig. 51b [cop. HUENE 1911].

1962 "*Mystriosuchus plieningeri* Meyer", Huene, 1911 – GREGORY [partim]: pp. 675, 677, fig. 4, tab. 2, non pp. 676 "broken fragments of phytosaur teeth", 677 "original specimens" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non pp. 676, 677 "*Belodon plieningeri*" [= *Nicrosaurus* species B]. [1962a].

1962 *Mystriosuchus plieningeri* – GREGORY: p. 17. [1962b].

1963 *Belodon plieningeri* – WESTPHAL [partim]: fig. 5 top, non fig. 3 [= *Nicrosaurus* species B]. [1963a].

1963 *Belodon plieningeri* H. v. MEYER – WESTPHAL [partim]: p. 163 "Rostrum", p. 164 "Schädelbreite, -höhe, -skulptur", fig. 1 top, non pp. 161, 162 "Meyer 1844: pl. 20 figs. 20-24, ?18-19" [= *Belodon plieningeri* v. MEYER, 1844, *nomen dubium*], non p. 163 ["Zähne, Unterkiefer MEYER (1965: pls. 46-47)", p. 164 "Squamosum" [= *Nicrosaurus* species B]. [1963b].

1968 *Belodon planirostris* H. v. MEYER – KUHN: p. 75, figs. 35(1-2), 36(3) [cops. HUENE 1911].

1969 *Mystriosuchus planirostris* – GREGORY [partim]: p. 46, non p. 42, non fig. 2 [= *Mystriosuchus planirostris* (MEYER, 1863)].

1969 *Mystriosuchus planirostris* (Meyer 1863) – GREGORY & WESTPHAL [partim]: p. 1296, non p. 1297 [= *Mystriosuchus planirostris* (MEYER, 1863)].

1971 *Belodon plieningeri* MEYER 1842 – KUHN [partim]: p. 14, figs. 24(3), 25(2-3) [according to captions], non p. 14 "Begleiter von *Nicrosaurus*" [= *Nicrosaurus* species B].

1976 *Belodon plieningeri* H. v. MEYER 1844 – WESTPHAL [partim]: p. 111 "Wucherungen, Squamosum", non p. 111 "Typus-Material" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non p. 111 "Merkmale", fig. 8e [= *Nicrosaurus* species B], non p. 111 "dorsaler Panzer", fig. 8d [= Phytosauria indet.].

1978 *Mystriosuchus planirostris* (Meyer), 1863 – CHATTERJEE [partim]: p. 115, tab. 3.

1985 *Belodon plieningeri* H. v. MEYER 1844 – MÜLLER [partim]: p. 317, fig. 384 [cop. HUENE 1911], non p. 317 "Kehlregion mit mosaikartiger Panzerung" [= Phytosauridae indet.].

1989 skull from Trossingen – HUNT & LUCAS: p. 340. [1989b]

1993 *Mystriosuchus* – BENTON & WILD: p. 37

1994 *Mystriosuchus* n. sp. – HUNT: 30A.

1995 *Belodon plieningeri* – HUNGERBÜHLER [partim]: p. 70, fig. 4, non p. 70 "Phytosaurierzähne" [= *Belodon plieningeri* MEYER, 1844, *nomen dubium*], non p. 70 "neugefundene Schädel" [= *Nicrosaurus* species B].

1995 *Mystriosuchus* sp. – LONG & MURRY: p. 38.

Holotype: GPIT 261/001, complete skull lacking the mandible (Figs. 3.3 - 3.9).

Type locality: former quarry "Untere Mühle", Trossingen, southern Württemberg (Fig. 1.1).

Type horizon: Upper Triassic, Middle Keuper, Stubensandstein, middle Stubensandstein, sandstone subunit sc3.

Age: Lower (or Middle) Norian.

Referred specimen:

GPIT 261/17/7, mid-section of the premaxillar part of a large snout, showing a complete premaxillary crest (HUENE 1911: pl. 17 fig. 7; this study, Fig. 3.10), from the Aixheim region is definitely referable to this species.

Other remains which may belong to this species include (see part 3.3.2.2):

GPIT 2145.000, a postsymphyseal fragment of a mandibular ramus (Fig. 3.11). Aixheim region.

GPIT 2146.000, a postsymphyseal fragment of a right mandibular ramus (Fig. 3.12). Former quarries at Neuhaus.

GPIT 2156.000, the imprint of a palatal snout fragment. Provenance unknown, but the matrix is consistent with that associated with vertebrate fossils from the Aixheim region.

Diagnostic characters (see discussion in part 3.3.4.1): alveolar ridges much more prominent than in *Mystriosuchus planirostris*; alveolar ridges semi-circular in cross-section in anterior part of the premaxillae; parietal process of the squamosal joins the descending lamina of the parietal-supraoccipital complex; lamina of the squamosal extends onto the anterior face of the paroccipital process and contacts the prootic; extension of the squamosal processes of the parietal lobate; posttemporal fenestra reduced to slit.

Summary description (diagnostic characters excluded): large species of *Mystriosuchus* with a skull length in excess of 1000 mm; rostrum massive, the length equals two times the narial + postnarial length; premaxillary crest present; gentle slope of the prenarial area; additional paired ossification posterolateral from the parietal separating the parietal from the squamosal ("supernumerary occipital bone"); no posterior process of the squamosal; paroccipital process of the squamosal is the posteriormost projection; extremity of the squamosal blunt; parietal process of the squamosal borders the posttemporal fenestra dorsally; foramen quadrati smaller than in *Mystriosuchus planirostris*; recess of the quadrate foramen distinctly triangular; supraoccipital reaches the posttemporal fenestra; exoccipitals united basally behind the foramen magnum; large foramen for the vena capitis dorsalis; prootic foramen entirely within the prootic; discrete orbitosphenoid

anterior to the laterosphenoid; alveoli much larger and more closely spaced than in *Mystriosuchus planirostris*; dentition probably bipartite heterodont, leading to a convex ventral margin of maxilla.

Distribution: region around Trossingen and Aixheim (southern Württemberg; Fig. 1.1).

Stratigraphic range and age: as GPIT 261/001.

3.3.2 Description

GPIT 261/001 is the most impressive and best preserved skull among the material under study, and probably the most informative phytosaur specimen yet known from Europe. The detailed description by HUENE (1911) makes the taxon one of the best known phytosaurs, the others being *Brachysuchus megalodon* (CASE 1929) and *Smilosuchus gregorii* (CAMP 1930). However, the original description is to some extent not detailed enough to allow a meaningful comparison with *Mystriosuchus planirostris*. GPIT 261/001 was described at a time when knowledge of phytosaur cranial anatomy was still in its infancy. The first "modern" comprehensive accounts on this subject were presented by MCGREGOR (1906) for *Mystriosuchus planirostris* and LEES (1907) for *Paleorhinus bransoni*, although both authors had to base their descriptions on more incompletely preserved and less accessible material. Hence, in 1911 HUENE had just a few not fully adequate publications at his disposal to compare with his reconstructions of the palate, braincase, and endocranial structures. HUENE described in a number of features which, in the light of our present knowledge, differ fundamentally from the configuration in other phytosaurs and consequently have been subject to criticism or led to considerable confusion. These features, if taken for granted, would markedly distinguish *Mystriosuchus* species B from its sistertaxon, *Mystriosuchus planirostris*, and could even lead to a suggestion to place the taxon in a genus of its own. The objective of this section is to reexamine those debatable characteristics of *Mystriosuchus* species B (snout protuberances, prechoanal region of the palate, the pterygoid, the area surrounding the supratemporal fenestra, and details of the endocranium).

A full redescription of the temporal region and the braincase of GPIT 261/001 is given. The anterodorsal part of the braincase and the internal palatal configuration, which in parts have been previously described, but only partially figured when the skull was still disassembled and under preparation, are hardly accessible without major intrusive

measures and a redescription has for this reason to await urgently needed conservation treatment of the specimen. For further information on the osteology of the remaining skull areas, with the exception of the above listed structures wherein my reinterpretation differs considerably from HUENE's (1911) view, I refer to the initial description.

3.3.2.1 The cranium

Snout

Premaxillary crest. GPIT 261/001 has a distinct premaxillary crest (Fig. 3.4), although the structure is distorted because the premaxillae have been laterally deformed in this area. Additionally, the bones are widely separated along the midline, and the right premaxilla was pushed downward revealing the joint surface of the left premaxilla. The length of the crest is approximately 150 mm extending dorsally from the alveoli pm (9) or pm (10) to pm (17) or pm (18), and reaches a maximum height of 25 mm. The accurate position is difficult to estimate because of the gently sloping crest line. The crest is set along the midline of the premaxillae, while the premaxillae show their normal convex shape below. The flanks are steep and converge dorsally, but the crest top is still rounded.

The premaxillary crest is much more impressive in the snout fragment GPIT 261/17/7 (HUENE 1911: pl. 12 fig. 7). While showing the same dimensions as the type skull, in contrast to the statement by HUENE (1911), the crest has steeper anterior and posterior slopes and occupies the entire width of the snout. The crest top is sharp. The exact position of the crest on the premaxillae is indeterminable because of the incompleteness of the specimen.

Alveolar ridges. On the maxillae, the alveolar ridges of GPIT 261/001 are broad but flat elevations (HUENE 1911: pl. 12 fig. 2). More anteriorly, the ridges become very prominent structures that show an almost half-cylindrical cross-section (Fig. 3.10), and the entire height may be exposed in lateral view (HUENE 1911: pl. 17 fig. 7). Another peculiarity is noticed in the configuration of the ridges on the palatal surface. Being widely spread apart immediately in front of the choanae, both alveolar ridges converge rapidly in the anterior direction, until they almost contact and then run parallel to each other in the middle and anterior part of the premaxillae (Fig. 3.10). Thus, the interpremaxillary fossa is considerably reduced in width to a narrow, slit-like groove with a V-shaped cross-section, at least in the anterior half of the snout.

Snout profile. In front of the nares, the snout slopes down in a straight line at an angle of about 40° and then levels gently to form a less elongated and more massive rostrum than in *Mystriosuchus planirostris* (compare Fig. 3.4 with Fig. 3.1). The outline of the snout profile immediate to the nasal openings remains convex, which is a plesiomorphic trait in comparison to *Mystriosuchus planirostris*.

Naris. The nares are large compared to the length of the whole skull. The external nasal opening is inclined anterodorsally throughout its length, in contrast to the naris of *Mystriosuchus planirostris* that faces upward in its posterior part, but almost forward anteriorly. The posterior part of the narial rim is in both species distinctly raised. In *Mystriosuchus* species B, a narial wing is also developed at a point about one third of the narial length behind the anterior rim of the naris, but with a vertical step of c. 8 mm the wing is comparatively small (Fig. 3.4). The internarial septum is comparatively broader, showing a constriction at mid-length. Posteriorly, the septum is below the lateral rim of the naris, but because of the development of the narial wing, the septum reaches the level of the rim in the anterior part of the naris. Since the anterior narial region is pathologically deformed (see HUENE 1911), there is no conclusive evidence for a rectangular shape of the internarial septum.

Dentition. The majority of the teeth once present in the specimen are now lost, and most of the information on the dentition must rely on the accuracy of HUENE's (1911) description. The alveoli are tightly-spaced throughout the jaws, much more so than in *Mystriosuchus planirostris*. The premaxillary teeth were apparently uniform in size, and since there is no significant enlargement of the posterior premaxillary alveoli, the dentition was probably bipartite. The premaxillary teeth show a round cross-section, but, in contrast to *Mystriosuchus planirostris*, they had less well developed fluting and two faint mesial and distal carinae. This applies also to two preserved maxillary teeth, but little is known about the dentition in the maxilla, apart from the smaller size of the first four or five alveoli. The following maxillary teeth were probably not considerably enlarged, in contrast to the suggestion of LONG & MURRY (1995). The high maxillary tooth shown *in situ* in HUENE (1911: fig. 2, pl. 8 fig. 1) was found dislocated in the right infratemporal opening of the specimen and was later inserted in an appropriate alveolus in the anterior part of the maxilla (HUENE 1911: 76). The tooth is now broken off at the base and not available for study any more, but I am not convinced from HUENE's description, figures, and the morphology of its preserved counterpart, that it belongs to the specimen or that it even can be referred safely to a phytosaur. The size of the alveoli suggests, however, that somewhat larger teeth were located in the posterior section of the maxilla. The convex alveolar margin of the maxilla also points toward a larger, more differentiated posterior

maxillary dentition. In summary, as far as can be concluded from the evidence available at present, *Mystriosuchus* species B had a dentition with tooth shapes comparable to that of *Mystriosuchus planirostris*, but the teeth were clearly proportionally enlarged. However, *Mystriosuchus* species B is a potential candidate for isolated, large and highly differentiated posterior maxilla (and dentary) teeth, which occur not infrequently at the sites around Aixheim.

Temporal region

Postorbito-squamosal bar: The postorbito-squamosal bars diverge posteriorly at an angle of 20° to the median axis of the skull. The lateral and medial rims are parallel. A cross-section of the right postorbito-squamosal bar of GPIT 261/001 is illustrated in Figure 3.6. The dorsal surface is convex, sloping down at 15° laterally. The internal surface of the bar is steeply inclined (c. 60° to the horizontal plane) and for this reason actually faces ventromedially. In its dorsal part, a narrow section of the bar is somewhat deflected toward the horizontal plane, but the internal face remains inclined and there is no distinct horizontal extension as in *Nicrosaurus*, *Pseudopalatus*, and *Arribasuchus*. Thus, the postorbital and squamosal overhang the medial side of the supratemporal fenestra for only 10 mm, and the fenestra is almost fully open dorsally (Fig. 3.5). The ventrolaterally facing rim of the infratemporal fenestra is deep as well (20.5 mm), and bears a prominent lateral squamosal ridge on the edge between the dorsal and lateral face, and a faint second ridge placed about in the middle of the surface. Hence, because of the orientation of the three surfaces, the postorbito-squamosal bar is a compact structure with a triangular cross-section, and considerably thickened in dorsoventral direction (Fig. 3.6).

The postorbito-squamosal bar is sculptured with elongate shallow grooves lacking a preferred orientation and deep pits typical of the skull roof and narial area. For this reason, GPIT 261/001 does not show a raised rounded rim along the lateral border of the supratemporal fenestra that result from the much deeper sculpture of the postorbito-squamosal bar characteristic of *Mystriosuchus planirostris*.

Squamosal. Like the postorbitosquamosal bar, the dorsal surface of the posterior part of the squamosal remains consistently broad. At the level of the tympanic recess, the lateral rim of the squamosal turns inward, which leads to a blunt and somewhat bulbous extremity of the bone. There is no pointed tip of the squamosal, nor is there a distinct posterior knob, as occurs in *Mystriosuchus planirostris*. A large, concave surface is demarcated on the side of the squamosal between the dorsal surface and the paroccipital process, which accounts chiefly for the considerable height of the squamosal body in

lateral view (Fig. 3.4). The surface is mainly aligned in a dorsolateral plane, but as a result of the inward bend of the lateral squamosal rim, it also faces somewhat posteriorly (Fig. 3.5). In contrast to the corresponding, but dorsolaterally to laterally facing area in *Nicrosaurus*, the surface is entirely smooth and is not subdivided by ridges into several distinct muscle attachment areas. The area terminates ventrally in two lobes with a ragged ventral outline, which slightly overhangs the sides of the skull. A posteroventral lobe is braced against the dorsolateral edge of the extremity of the opisthotic. A similar anteroventral lobe occurs just above the tympanic fossa.

The posteriormost point of the squamosal is marked by its well developed paroccipital process (Fig. 3.4), a condition that is found only in one specimen of *Mystriosuchus planirostris* (SMNS uncat. no. 184). However, the tip of the squamosal of GPIT 261/001 terminates exactly above the posterior surface of the paroccipital process of the opisthotic. Hence, the squamosal does not extend behind either the level of the basioccipital condyle or the posterior extremity of the quadrate as in all *Mystriosuchus planirostris*, and thus there is no posterior process of the squamosal developed as defined above.

HUENE was most probably right in reconstructing the parietal process of the squamosal as longer than in any other phytosaur. The process separates from the body of the squamosal in the form of a broad, but extremely thin lamina and curves ventrally and medially to form a horizontal plane on the paroccipital process. Thus, a deep, triangular posteriorly facing recess is present above the extremity of the paroccipital process of the opisthotic, roofed, from medial to lateral, by the parietal process, the slight overhang of the squamosal tip and the inclined lateral surface of the squamosal (Fig. 3.5). The process roofs the lateral part of the posttemporal fenestra and continues onto the lateral extremity of the supraoccipital. At the flank of the supraoccipital shelf, the parietal process is transformed into a sharp vertical lamina and terminates in an intimate interdigitation with the supernumerary occipital bone (Fig. 3.5; Fig. 3.7).

An anteroventral lamina of the parietal process covers the anterolateral face of the paroccipital process, just as in *Nicrosaurus kapffi* SMNS 4378. The lamina even extends inward and forward as far as to the prootic, and by this separates the externally visible surface of the opisthotic into two areas (Fig. 3.9).

Palatal region

Vomer. There is only little evidence for the enormous lateral extension of the vomer in front of the choanae between premaxilla, maxilla, and palatine as described and figured in HUENE (1911: 16-17, pl. 12 fig. 2). On the right-hand side, the maxillo-vomeral suture identified by HUENE is actually a fissure, present only in the posterior part

of the alleged contact between the two bones. This is the approximate position of similar fractures occurring in *Nicrosaurus* (see *Nicrosaurus* species B, subsection 2.3.3). Hence, in *Mystriosuchus* species B a configuration of the prechoanal palate is present which is common among phytosaurs, with the maxilla sending a process posteromedially to contribute broadly to the choana (see *Nicrosaurus kapffi*, part 2.2.3.3; CAMP 1930; CASE 1929).

Pterygo-quadrate plate (Fig. 3.5). The contact between pterygoid and quadrate is an almost vertical plate running in an anteromedial direction. In posterior view, a comparatively large ventral part of the plate is deflected into a horizontal position. In contrast to *Nicrosaurus kapffi*, there is no furrow along the medial rim of the deflected shelf. The pterygoid wing of the quadrate is triangular, the blunt apex pointing anteriorly, and forms the majority of the pterygo-quadrate plate in terms of thickness. It extends anteriorly to the level of the trigeminal foramen. The pterygo-quadrate suture is well distinguished on the right-hand side only in Figure 3.5: the suture is somewhat disarticulated and filled with matrix. The left side is obscured by a coating of plaster. A posterolateral extension of the quadrate wing of the pterygoid covers the deflected area of the pterygo-quadrate plate in posterior view. A second dorsolaterally trending process can be seen extending along the pteroccipital fenestra (Fig. 3.5; Fig. 3.9).

This is basically the same configuration as in *Nicrosaurus* and *Mystriosuchus planirostris* (see Figs. 2.14, 2.25, 2.54; MCGREGOR 1906: fig. 5). There is no conclusive evidence at all that the quadrate wing of the pterygoid extends far back to the quadrate foramen (as reconstructed by HUENE 1911: fig. 3) or even appears on the lateral side of the cheek (HUENE 1911: fig. 2). On both sides of GPIT 261/001, the crucial areas have been either fully restored or are, in parts, superficially covered with plaster. The posterior outline of the pterygoid according to HUENE is interpreted here as both a misinterpretation of fractures (HUENE 1911: fig. 3, transverse quadrate-pterygoid suture) and as representing the standard course of the sutures between quadrate and quadratojugal, and quadrate and squamosal in a phytosaur.

Occipital region

Parietal-supraoccipital complex. The parietal-supraoccipital complex is higher and more slender than in *Nicrosaurus*, but there are no differences in the shape and size to that of *Mystriosuchus planirostris* (compare MCGREGOR 1906: fig. 5 to Fig. 3.5). The left descending lateral lamina of the parietal in GPIT 261/001 is deformed and pushed inwards at mid-height, leading to an unnaturally constricted appearance of the parietal-supraoccipital complex.

Parietal. At the top of the parietal-supraoccipital complex, there is a posteriorly rounded, large ledge overhanging the supraoccipital shelf (Fig. 3.5). The squamosal processes of the parietals are laterally compressed laminae that descend vertically. Just below the ledge, they form two lobe-like extensions projecting posteriorly (Fig. 3.7).

Supernumerary occipital element. By contrast to *Mystriosuchus planirostris*, most of the descending lateral lamina of the parietal-supraoccipital complex is actually formed by a separate ossification and the parietal process of the squamosal. This ossification is correctly outlined in HUENE (1911): on the supraoccipital shelf, the bone is firmly united with the squamosal process of the parietal, the supraoccipital, and the parietal process of the squamosal by strongly indentated sutures (Fig. 3.5). The bone thus fully separates the parietal from the squamosal, at least at the surface. A careful re-examination of this area resulted in the conclusion, that this is most likely the genuine condition, rather than the result of erosion. On the lateral side toward the supratemporal fenestra (Fig. 3.7), the ossification slopes steeply ventrally, framed by the parietal and squamosal, to meet the laterosphenoid and the prootic. There are also indications of a further skull element participating at the ventral border (see below). HUENE (1911) named the bone of the supraoccipital shelf the epiotic. It is referred to here as the supernumerary occipital bone, and its affinities are discussed in part 3.3.3.3.

Supraoccipital. The supraoccipital (Fig. 3.5) is drawn out laterally to a thin and slender process that underlies the parietal process of the squamosal. It reaches the posttemporal fenestra and borders the dorsal medial half of this opening. The posttemporal process of the supraoccipital is not discernible in anterior view (Fig. 3.7). A comparatively narrow ventral extension of the supraoccipital contributes to the roof of the foramen magnum, separating the exoccipitals for only a short distance.

Paroccipital process (Fig. 3.5). The posterior ridge of the paroccipital process is remarkably prominent and divides the medial part of the posterior face into a posterodorsal and posteroventral plane. The ridge curves downward and merges with the medial end of the ventral opisthotic ridge. The ventral ridge of the opisthotic is rather weakly developed and there is only a slight dorsolateral extension of the lateral half of the process. HUENE (1911: 21) described the course of the exoccipital-opisthotic contact on the posterior face of the paroccipital process in detail. At least the horizontal section can be fully corroborated. The continuation of the suture onto the ventrally curved face of the process is not clearly indicated in the specimen. It is concluded that the exoccipital and opisthotic are only partially fused in GPIT 261/001, and the specimen is to my

knowledge one of only three phytosaurs (the others being *Mystriosuchus planirostris* SMNS 10260 and SMND 13007) that shows an externally persistent exoccipital-opisthotic suture in this area.

Posttemporal fenestra. The posttemporal fenestra of *Mystriosuchus* species B (Figs. 3.5, 3.9) is even more reduced than in its sister taxon. Preserved on the right-hand side only, it is a slit still filled with matrix that shows a maximum width of 13 mm and a height of less than 2 mm. The fenestra is almost invisible in posterior view, but its presence is indicated by a deep recess on the anterior face of the closely applied paroccipital process and parieto-squamosal bar.

Quadrate. With regard to the shape of the quadrate, there are no significant differences between *Mystriosuchus planirostris* and *Mystriosuchus* species B. However, the quadrate foramen in *Mystriosuchus* species B is comparatively smaller than in its sister-taxon. Furthermore, the quadrate foramen, as well as the recess formed by quadrate and quadratojugal, is triangular as in *Nicrosaurus*, in contrast to the perfectly circular shape in *Mystriosuchus planirostris*.

Braincase

Basioccipital. *Mystriosuchus* species B lacks a distinct "neck" of the occipital condyle (Fig. 3.8). The connective area between the basioccipital condyle and the basal tubera on the body of the basioccipital is concave ventrally, but almost as broad as the condyle itself. Since GPIT 261/001 is not significantly compressed dorsoventrally, this seems to be the genuine condition. The neck bears a rounded ventrolateral ridge on each side, and a longitudinal median ridge. The basal tubera are widely splayed, but are not clearly separated. They must have been linked (the left tuber of the specimen is only fragmentarily preserved, Fig. 3.8) by a narrower intertuberal ridge of almost equal height. The muscle insertion area of the basal tubera faces almost exactly ventrally. The suture with the basisphenoid runs transversely, separating the right basal tuber into two equally-sized halves. The contact with the exoccipital/opisthotic complex is a horizontal suture at the level of the dorsal rim of the condyle. Owing to the size of both the jugular and stapedial recesses, the basioccipital bears a broad channel leading from the jugular foramen onto the posterolateral area of the tuber. A similar structure though only half as wide, parallels the jugular depression from the foramen ovale along the basioccipital/basisphenoid suture, demarcating morphologically the basioccipital and basisphenoidal section of the basal tuber.

Exoccipital and opisthotic. Despite a short suture being visible on the paroccipital process (Fig. 3.5), the exoccipital and the neurocranial part of the opisthotic are indistinguishably fused elsewhere and for this reason treated together. The exoccipitals meet in front of the foramen magnum and exclude the basioccipital from the floor of the foramen (Fig. 3.5). The exoccipital pillar forming the lateral border of the foramen magnum is strongly developed. The singular foramen hypoglossus (XII) penetrates the exoccipital on the anterior face of the pillar (hidden from view in Figure 3.8), but is still about 10 mm from the jugular foramen (Fig. 3.9). The path of the nervus hypoglossus is indicated by a semilunate depression around the base of the exoccipital pillar (Fig. 3.9). The jugular and oval foramina are large and situated in two deep recesses, in lateral view separated by a sharp, very prominent opisthotic lamella (Fig. 3.8). However, the jugular groove and the much wider stapedial groove on the ventral face of the paroccipital process are less well defined as in both species of *Nicrosaurus*.

Basisphenoid. The basisphenoid sends a thin process upward, wedged between the exoccipital-opisthotic complex and the prootic toward the foramen ovale (Fig. 3.8), though it is not certain whether the basisphenoid actually reaches this opening. The internal carotid foramen lies deep on the lateral surface of the basisphenoid, horizontally aligned with the prootic foramen (Fig. 3.9). The relationships among the anterior parts of the basisphenoid, the prootic, and the parasphenoid are not entirely clear, so that the length of the ascending clinoid process of the basisphenoid is not determinable.

Epiotic. The lateral side of the supernumerary occipital bone is morphologically separated from the side wall of the braincase by a crescent-shaped, ventrally open crest that continues for a short distance on the posteroventral process of the parietal (Fig. 3.7). Underneath the ventral section of the crest, a large slit-like foramen pierces the braincase wall. The supernumerary occipital bone-prootic suture can clearly be seen entering the foramen from ventrally. However, there is no safe evidence for a suture between the supernumerary occipital bone and the anterior part of the epiotic dorsal from the foramen, though this might be obscured by the crest. This suggests that the anterior part of HUENE's epiotic (here named supernumerary occipital bone) is actually a separate ossification, and indeed homologous to the epiotic. This interpretation is strengthened further by the similar configuration of a bone usually referred to as the anterior part of the supraoccipital in "*Parasuchus*" (CHATTERJEE 1978), *Smilosuchus* (CAMP 1930), *Nicrosaurus* (this study, Fig. 2.7), and in an indeterminable phytosaur braincase (*Machaeroprosopus* sp., MEHL 1916). CAMP (1930: fig. 37, "for"), MEHL (1916: fig. 10), and CASE (1928: fig. 2, "n") also indicate the presence of a foramen in the same position for the genus *Leptosuchus*, though in all cases the foramen is much smaller than

in *Mystriosuchus* species B. According to the position, the vena capitis dorsalis probably left the braincase through this foramen (JANENSCH 1936; WALKER 1990).

Prootic. The posterior process of the prootic extends broadly onto the paroccipital process, forming the sharp and prominent anterior lamina of the foramen ovale and the lateral wall of the stapedial groove (Fig. 3.8). This anterior lamina is penetrated by the foramen of the facial nerve (VII) entering the braincase in an anteromedial direction. On both sides of the braincase, the complex serrated suture between laterosphenoid and prootic is clearly indicated in the extent of the prootic-epiotic contact, running horizontally forward on a line projecting from the base of the foramen opticum. The prootic foramen thus lies entirely within the prootic (Fig. 3.9). There is a narrow sinuous slit which divides the anterior part of the braincase into a dorsal and ventral section. The roof section of the slit belongs to the prootic. The slit leads gently upward from the prootic foramen and finally emerges at the anterior surface of the braincase just above the parasphenoid rostrum. This leads to the impression that the prootic foramen "communicates" with the orbital cavity by means of a passage. HUENE (1911) considered the missing part of the braincase broken off, but leaves the question open, whether the damage occurred before burial or during recovery of the skull. The chances, however, that an element of the braincase (e.g. the presphenoid, see subsection 3.3.3) is missing here, seem remote, since even the delicate epipterygoids next to the slit are preserved *in situ* and largely intact. Concerning recent damage, the concave surfaces of the gap do not show signs of fracturing such as sharp edges, and the braincase is otherwise fully intact. There are no sutures detectable on the bone surfaces surrounding the gap. The situation is more consistent with the assumption that the braincase of GPIT 261/001 was incompletely ossified in its anterior part, and the gap actually represents a cartilaginous zone. In analogy to "*Parasuchus*" and *Smilosuchus*, the hypophyseal foramen must have been situated within this passage, perhaps in the dorsal concavity of the roof seen in about the middle of the gap.

Laterosphenoid. HUENE did not recognise the prootic-laterosphenoid suture identified here (see HUENE 1911: fig. 7; however, he marked the corresponding suture on the opposite side of the braincase in red ink), and consequently referred large parts of the laterosphenoid to the prootic. The laterosphenoid proper in phytosaurs extends far forward along the median line of the skull below the dermal skull roof bones (CAMP 1930, CHATTERJEE 1978), and, according to HUENE (1911), in GPIT 261/001 the laterosphenoid is still preserved at the anterior border of the frontals. Limited accessibility to the ventral interorbital region prevents a close inspection. The posterior process of the laterosphenoid reaches backward to about the level of the prootic foramen, meets the

supernumerary occipital bone posterodorsally and embraces the epiotic (Fig. 3.9). The ophthalmic ramus of the trigeminal nerve (V_1) and the nerve to the m. levator bulbi in phytosaurs was possibly transmitted via a groove leading anteroventrally from the prootic foramen (CAMP 1930; CHATTERJEE 1978; see CLARK *et al.* 1993 and GOWER 1997 for other archosaurs). Since a groove in the corresponding position in GPIT 261/001 is very poorly defined anteriorly (Fig. 3.9), the path of the ophthalmic ramus is actually better described as a concavity below a ridge on the dorsal-most part of the prootic and the laterosphenoid. The course of the ridge is not straight, but markedly crescentic.

Orbitosphenoid. A vertically ascending suture is preserved on the right-hand side of the braincase just in front of the path for the ophthalmic ramus of the trigeminal nerve (V_1), that separates the laterosphenoid from an anteriorly placed discrete ossification. The suture can be seen continuing in an anterodorsal direction from the point where the ridge of the ophthalmic branch disappears (Fig. 3.9), but it was impossible to trace it further forward. Thus the anterior extent of the ossification remains obscure. The element is a paired ossification, showing a suture along the anterior margin of the braincase. For two reasons, there are uncertainties in establishing the presence of a separate ossification. Firstly, the preservation of the corresponding area at the left side of the braincase is too poor to permit a conclusive interpretation. Secondly, in this area of the braincase, two strut-like pillars, usually referred to as the capitate processes of the laterosphenoids (CLARK *et al.* 1993), frame the foramen opticum (II) and extend anteriorly and dorsally to buttress the skull roof (CAMP 1930: fig. 36; CHATTERJEE 1978: fig. 5a). The capitate processes tend to collapse under lateral compactive pressure, which would result in fractures at about the point of the suture described above. However, the braincase of GPIT 261/001 is not even deformed here (HUENE 1911: fig. 9). Huene also indicated the anterior border of the laterosphenoid in his fig. 8, but since he mistook the laterosphenoid as part of the prootic, he equated the anterior ossification with the "orbitosphenoid" (then the widely used name for the bone referred to as laterosphenoid in the modern literature on archosaurs, see CLARK *et al.* 1993).

Presphenoid. As discussed in the section on the prootic, there is no evidence preserved in *Mystriosuchus* species B for a separate presphenoid below the laterosphenoid-orbitosphenoid complex.

Parasphenoid. HUENE (1911: 84, figs. 6-8) reconstructed the cultriform process as being composed of a ventral parasphenoidal part (rostrum parasphenoidale) capped by a trough-like presphenoid (rostrum praesphenoidale). The same condition has only been reported subsequently in *Angistorhinus grandis* (MEHL 1913). Although there is clearly a

longitudinal groove along the flanks of the structure, I cannot find evidence for a suture in *Mystriosuchus* species B. Consequently, the whole structure is interpreted as the parasphenoid. This brings *Mystriosuchus* species B into line with the majority of phytosaurs in which the parasphenoid rostrum has been described ("*Parasuchus*": CHATTERJEE 1978; *Leptosuchus*: CASE 1922; *Smilosuchus*: CAMP 1930; *Angistorhinopsis*: HUENE 1922). The posterior demarcation of the parasphenoid from the prootic and basisphenoid is not visible.

3.3.2.2 Specimens possibly referable to *Mystriosuchus* species B

Description

GPIT 2145.000. This postsymphyseal fragment of a mandibular ramus (Fig. 3.11) has a length of 113 mm and a constant width of 35 mm. Neither the exact position in the jaw nor the anteroposterior direction is determinable. The fragment includes eight alveoli, which show diameters ranging from 10.5 to 12 mm. They are round, closely spaced and well separated from each other, although this is somewhat obscured because some interalveolar septa were broken off, presumably during recovery. A round tooth base (diameter of 5.3 mm) fills alveolus 5 (numbered from the bottom in Figure 3.11), and a second tooth fragment with an oval cross-section , the long axis (FABL 8 mm) parallel to the jaw, is situated in alveolus 7.

A 4 to 5 mm wide, deep groove with rounded, somewhat undulating edges parallels the tooth row at a distance of approximately 4 mm from the medial side. In dorsal view, the groove separates a 6 mm wide splint of bone, the dorsal part of the splenial, from the dentigerous part of the fragment. Dentary and splenial are united ventrally in a suture in continuation of the groove. It is unclear whether the groove is a natural feature, or whether it indicates that the splenial has been partially detached from the dentary. The slopes of the groove show no indication of being roughened sutural surfaces. Moreover, in contrast to the typical morphology of a phytosaur splenial, the splenial of GPIT 2145.000 maintains a constant width rather than tapering posteriorly, and the bone is not located next to the tooth row forming the medial walls of the alveoli (compare e.g. GPIT 2146.000 Fig. 3.12, and Fig. 3.11). Rather than a fracture, the groove is more likely to represent an equivalent of the paradental groove described in theropods (e.g. CHARIG & MILNER 1997), a feature, so far not described in a phytosaur mandible, that possibly transmitted nutrient blood vessels to the teeth.

GPIT 2146.000. This specimen consists of a 13.4 mm long fragment of a left mandibular ramus from close behind the symphysis, which includes the dentary and the

closely applied splenial on its medial side (Fig. 3.12). The anterior width of the fragment (28 mm) tapers continually to the posterior end, where the jaw shows the maximum height of 29 mm. The dentary contains 14 alveoli. The anterior ones are round, c. 10 mm in diameter, and well separated. Posteriorly, the alveoli become oval, the long axis (11.5 mm) oriented transversally, and tend to merge by resorbtion of the interalveolar septae. The anteriormost alveolus is cut in half by a fracture, and reveals an unerupted replacement tooth. The tooth base is round and a faint, unserrated carina is seen running along the preserved tooth crown height. At mid-height of the dentary, the bone shows the lateral dentary groove, which in this part of the jaw is subdivided in a line of separate elongated pits fading away near the end of the fragment. The splenial, being 11 mm wide at the anterior end of the fragment, tapers markedly to a width of approximately 2 mm posteriorly.

GPIT 2156.000. This specimen consists of the imprint of the right half of the palatal surface of an upper jaw, presumably a right premaxilla, consisting mainly of a mould of the alveolar ridge with some fragmented bone tissue referable to the interpremaxillary fossa. The ridge has width of 16.5 mm, which is consistent with *Mystriosuchus* species B GPIT 261/000 and GPIT 261/17/7. The basal cross-section of one tooth is preserved to the right of the alveolar ridge. Its outline is subrectangular, fore-aft basal length being 13 mm and basal width 9 mm.

Discussion of the affinities of the fragments

The only phytosaur taxa from the Stubensandstein of the Aixheim region known from cranial remains are *Mystriosuchus planirostris*, represented by numerous complete skulls, and *Mystriosuchus* species B. The large size of the mandibular fragments, the diameters of the alveoli around 10 mm or more, and the tight spacing of the teeth in all three specimens suggest that these specimen belong to a single taxon. These characters, and the width of the alveolar ridge in GPIT 2156.000 is not coincident with mandibles referable to *Mystriosuchus planirostris*, as represented by e.g. SMNS uncat. no. 180 and 183. By contrast, the same features characterise the premaxilla and maxilla of GPIT 261/001, and are also present in GPIT 261/17/7. The resemblance regarding the jaw morphology, and the identical provenance therefore suggest that the mandibular fragments are referable to *Mystriosuchus* species B. However, such a robusticity of the jaws, plus alveolar size and tooth spacing characterise all large, deep-snouted phytosaurs (CAMP 1930; CASE 1930; subsection 2.2.4). It cannot be excluded by morphological evidence that, alternatively, the fragments indicate the presence of a second robust phytosaur taxon at Aixheim, although this possibility seems remote for palaeoecological

reasons and regarding our knowledge of phytosaur assemblages (HUNT 1989; LONG & MURRY 1995). The structure of GPIT 2145.000 resembling a paradental groove is not present in *Mystriosuchus planirostris* (pers. obs.), nor in all large phytosaur taxa of which the mandible is known. Only future finds will show whether this a derived feature of *Mystriosuchus* species B, characterises a so far unknown phytosaur taxon, or represents a preservational artefact.

3.3.3 Discussion

3.3.3.1 The premaxillary crest

The raised areas on the premaxillae of GPIT 261/001 and GPIT 261/17/7 have previously been interpreted as individual pathological abnormalities (HUENE 1911; ABEL 1923; GREGORY 1962a). There are, however, several criteria which are in conflict with this interpretation.

(a) A premaxillary crest is also present in at least one specimen of (?) *Nicrosaurus* species B (SMNS uncat. no. 11; Fig. 2.63), meaning that such a structure in *Mystriosuchus* species B is by no means unique within Phytosauria. Additionally, humps on the premaxillae are not uncommon among various phytosaur taxa (CASE 1929), and in some specimens the elevation may well achieve the dimensions of a premaxillary crest (e.g. CASE & WHITE 1934: pl. 1).

(b) The surface texture of the disarticulated interpremaxillary suture in GPIT 261/001 in the region of the premaxillary crest is similar to that seen in the prenarial crest of *Nicrosaurus* species B SMNS uncat. no. 11 (Fig. 2.64).

(c) The presence of a premaxillary crest does not affect the course of the straight interpremaxillary suture, in contrast to the possibly pathologic cavities and protuberances on the prenarial crests of *Nicrosaurus kapffi* (e.g. Figs. 2.12, 2.15).

(d) In both specimens of *Mystriosuchus* species B, the crest is located in approximately the same position on the premaxilla (HUENE 1911: pl. 12 fig. 1 and pl. 17 fig. 7).

(e) The premaxillary crests in both specimens are always in the midline of the snout (MOODIE 1922). This applies also to specimens that show premaxilla humps.

(f) In contrast to a statement by ABEL (1923), the premaxillary crest is bilaterally symmetric in GPIT 261/17/7 (MOODIE 1922) and SMNS uncat. no. 11, and the

asymmetry in GPIT 261/001 can be attributed to *post-mortem* distortion. This is not the case in the pathological prenarial cavity of GPIT 261/001 (HUENE 1911: pl. 13 fig. 1).

These features support an identification of the eminencies in *Mystriosuchus* species B (GPIT 261/001 and GPIT 261/17/7) as natural premaxillary crests. For a definitive solution of this issue, a histological study of the crest structures in phytosaurs might offer the most promising approach.

3.3.3.2 Orbitosphenoid

In GPIT 261/001, a separate ossification is found in the same position occupied by the anteroventral part of the laterosphenoid in "*Parasuchus*" (CHATTERJEE 1978: fig. 5) and *Smilosuchus* (CAMP 1930: fig. 36) just above an unpaired element termed presphenoid by these authors. However, in a paper ignored in the subsequent literature on phytosaurs, CAMP (1942: 33, fig. 21) revised his reconstruction of the anterior part of the braincase of *Smilosuchus* and presented new, corroborating evidence from *Leptosuchus*. The phytosaurian laterosphenoid (*sensu* CAMP 1930) is subdivided into a laterosphenoid *sensu strictu*, an anteriorly placed orbitosphenoid, and a "septosphenoid" enclosing the anterior part of the olfactory tract. CAMP's (1942) configuration of the laterosphenoid and orbitosphenoid corresponds to, and thus supports, the interpretation of *Mystriosuchus* species B presented here. Furthermore, CAMP suggested that the laterosphenoid *sensu strictu* and orbitosphenoid fuse to the bone commonly identified as the laterosphenoid, based mainly on the observation that traces of the sutures persist in internal aspect, but seem to be obscured by laminar bone externally. This would explain the observed discrepancies within Phytosauria. This suggestion, however, needs to be tested by studies of dissociated material or braincases of juvenile individuals, not only in phytosaurs, but archosaurs in general, since CAMP (1942) tentatively extended his interpretation to crocodiles, and arrived at the conclusion that the archosaurian laterosphenoid is a composite bone.

The laterosphenoid bone is one of the synapomorphies of the Archosauria in their traditional composition (CLARK *et al.* 1993, their clade Archosauriformes). There is no evidence for a further ossification in the anterior braincase of basal archosaurs below the crown-group Archosauria + *Euparkeria*. Among crurotarsans, an additional ossification in a similar position to that in GPIT 261/001 has been reported in aetosaurs only, and was identified as the orbitosphenoid (PARRISH 1994). The crown group Crocodylia lacks such an individual orbitosphenoid (IORDANSKY 1973), and there is no evidence for the

bone in crocodylomorphs (WALKER 1990). The orbitosphenoid seems to be more widespread among Ornithodira. It is most likely present in birds (BAUMEL & WITMER 1993), although there is some controversy about the number of ossifications in the anterior part of the braincase and the interorbital septum in this group (JOLLIE 1957). In the fossil members of Ornithodira, a separate paired ossification in a position around the foramen opticum has been described in pterosaurs (KELLNER 1996) and a variety of dinosaurs (for instance, MADSEN 1976; TAQUET & WELLES 1977; CURRIE 1985; CURRIE & ZHAO 1993a, b).

However, there are a number of uncertainties involved. Firstly, the reported presence of such an ossification within fossil archosaurs in the clades Pterosauria, Aetosauria, and now Phytosauria, is severely hampered by the observation, that in none of the specimens can the element in question be fully segregated from surrounding braincase elements. Concerning the two reports in pterosaurs, the orbitosphenoid is either indicated by dashed sutures only (KELLNER 1996: fig. 6), or the area is said to be severely damaged (KELLNER 1996: 17). It is not entirely clear, and has yet to be demonstrated convincingly, that this area is not part of one of the well known braincase bones, but really represents a separate ossification. Although a suture between orbitosphenoid and laterosphenoid in the aetosaur *Longosuchus* is mentioned in the text, it is not indicated in the figures (PARRISH 1994: 201, figs. 4-5). The presence of an orbitosphenoid in aetosaurs, however, is supported by the report from the genus *Desmatosuchus* presented in the same study.

Much more serious are the widely differing and confusing opinions on the homology of the ossifications occurring in the posterior region of the orbit and the area of the interorbital septum. A number of elements may ossify in the embryonic orbitotemporal cartilage (RIEPPEL 1993b). Among Recent sauropsids, JOLLIE (1960) lists the occurrence of ossifications termed mesethmoid (within the interorbital septum), presphenoid, orbitosphenoid, laterosphenoid, and pleurosphenoid (all of them in the anterior braincase around the foramen opticum), rarely also apparently independently evolved membranous bones (CLARK *et al.* 1993). The numbers of endochondral ossifications may differ markedly, and various combinations of names have been employed (e.g. CLARK *et al.* 1993: tab. 1). There seems to be a consensus in the assumption that the various elements around the exit of the optical nerve (II) represent individual ossification centres of the single sphenethmoid of primitive amniotes (JOLLIE 1960). However, which of these separate ossifications are homologues across amniotes or whether additionally neomorphous bones have been incorporated into the orbit and anterior braincase (and if so, which of the separate ossifications are neomorphous) is still an unsolved question. For example, the presphenoid *sensu* CURRIE (1985) in Theropoda

(in a position similar to the mammalian presphenoid, STARCK 1979) is topologically dissimilar to the presphenoid of CAMP (1930) and CHATTERJEE (1978) in Phytosauria, and therefore these bones are unlikely to be equivalent. Such incongruences represent a serious problem for phylogenetic interpretations.

The criterion of topology (including the location around the foramen opticum, position anterior and ventral to the laterosphenoid) supports the equivalence of the elements in question in *Mystriosuchus*, *Longosuchus*, *Desmatosuchus*, and Dinosauria. The posterior part of the structure is, however, much more prominent in the aetosaurs, and the considerable anterior extent as in *Longosuchus* is unknown for *Mystriosuchus*. The element in *Mystriosuchus* shows more topographical similarities (size, shape) with the theropodan ossification in similar position (e.g. TAQUET & WELLES 1977; CURRIE 1985), but at least partially fails the criterion of position in not contacting the prootic. These are considered here but minor differences. For conventional reasons, I follow the majority of studies on archosaurian braincases and use the term orbitosphenoid for the element in front of and ventral to the anterior process of the laterosphenoid.

3.3.3.3 Supernumerary occipital bone

A discrete element, corresponding to the posterior part of a bone identified as the epiotic by HUENE (1911), is present in the occipital region in GPIT 261/001 (Figs. 3.5, 3.7). An element in similar position has been identified as a tabular in the description of the type of *Smilosuchus gregorii* (CAMP 1930). An attempt to find out, whether, firstly, the supernumerary bone and CAMP's tabular are homologous with each other, and, secondly, to which skull element in amniotes they correspond, requires a review of their positional relationships and the structure in both specimens:

- In occipital view, the supernumerary bone of GPIT 261/001 occupies virtually the same position as the tabular in CAMP (1930: figs. 29-30, pl. 5) and the lamina of the squamosal process of the parietal onto the supraoccipital in, for example, *Nicrosaurus kapffi* (see part 2.2.3.3; Fig. 2.41). Like the element in *Smilosuchus gregorii* (CAMP 1930: fig. 37), the supernumerary bone rides on the supraoccipital and extends onto the medial surface of the posterior part of the braincase.
- As in CAMP's (1930: 97; pl. 5) tabular, the element in *Mystriosuchus* species B is fully integrated in the parieto-squamosal bar and interrupts the continuity of the parietal and squamosal.
- Both elements in question have the same triangular transverse cross-section.

Whereas in *Smilosuchus gregorii* and *Mystriosuchus* species B the positional relationships of the ossifications in question are the same, there are structural differences regarding these bones between GPIT 261/001 and *Smilosuchus gregorii*. The same differences are noted in the comparison of *Mystriosuchus* species B with other phytosaurs, if the projections of the lamella of the squamosal process of the parietal onto the supraoccipital shelf is regarded as an equivalent:

- The supernumerary bone in GPIT 261/001 is stouter and occupies a far less extensive area on the supraoccipital shelf than the tabular in *Smilosuchus gregorii*. The part of the supraoccipital shelf formed by the posterior section of the tabular in *Smilosuchus gregorii* is occupied by the medial extremity of the squamosal in *Mystriosuchus* species B.
- In GPIT 261/001, the sutures of the supernumerary bone with the supraoccipital are not smooth, but complexly serrated, which does not correspond to the model of a lamella or a superficial dermal bone. The internal extent and the relationship of the bone to the brain and otic cavities cannot be determined and may differ as well. The bone, however, appears to be more firmly integrated into the otic and occipital parts of the neurocranium than the ossification in *Smilosuchus gregorii*.

Based on the positional similarity, it is concluded that the additional bone in *Mystriosuchus* species B above the supraoccipital and interrupting the unity of the parieto-squamosal bar, an element in a similar position in *Smilosuchus gregorii*, and the lamina of the squamosal process of the parietal in other phytosaurs are positional equivalents, despite minor structural differences. Thus, they are probably homologous elements.

It is much more difficult to establish a homology with distinct ossifications that occur in the occipital region of primitive amniotes. No archosaur shows a discrete ossification in the occipital region and in the same position. CAMP's identification is one possibility, but there are a number of potential equivalents of the "supernumerary" occipital bone in *Mystriosuchus* species B and *Smilosuchus gregorii*, other than a tabular, that need to be discussed. Finally, the elements could also represent a newly evolved bone unique to phytosaurs, or an ingroup within phytosaurs.

(a) Epiotic. The usual definition of the epiotic as a replacement bone lying dorsally to the otic capsule does correspond to the element in question in GPIT 261/001. The epiotic is still recognisable as a separate ossification in early embryonic stages in *Alligator*, but later fuses with the supraoccipital (RIEPPEL 1993a). This supports the suggestion that the element is also present in fossil crurotarsans, and an epiotic (referred

to as part of the supraoccipital) has been identified in phytosaurs (CAMP 1930; CHATTERJEE 1978). There is also the possibility that the epiotic may have persisted as a distinct bone in the braincase in later ontogenetic stages. However, in *Mystriosuchus* species B a second separate ossification anteroventral to the bone in question corresponds to the definition given above, and is suggested here as the homologue of the epiotic in this species. HUENE's (1911) interpretation of the supernumerary bone in GPIT 261/001 as an epiotic is only plausible, if the individuality of the element dorsal to the supraoccipital (here the supernumerary bone), and the element anterior to it (here the epiotic), is not accepted.

(b) Postparietal and dermo-supraoccipital. In primitive amniotes, the postparietals are paired median elements of the skull roof situated directly posterior to the parietals (ROMER 1956). Usually the postparietals are in contact with each other, but they tend to fuse in numerous taxa (DEBRAGA & RIEPPEL 1997). Furthermore, each postparietal is situated dorsally or medially to the tabular. The topographical relationship to the tabular is not applicable here. The criterion of the relative position to the parietals is contradicted by the evidence in GPIT 261/001, in which the supernumerary bones are situated posteromedial of the parietals. Moreover, the paired elements do not establish contact but are well separated. Both conditions also apply to the even larger paired elements of *Smilosuchus*.

These criteria are, however, in accord with a large unpaired element covering the supraoccipital shelf in *Smilosuchus gregorii* (CAMP 1930) and *Francosuchus angustifrons* (KUHN 1936), equated by both authors with an interparietal. An element identified as a right postparietal was recently reidentified in embryonic alligators (KLEMBARA 1997). However, there is still confusion about the nature and identity of the crocodilian postparietal with an unpaired bone named dermo-supraoccipital in a similar position (see RIEPPEL 1993a).

(c) Tabular. The tabulars are paired dermal elements, which in primitive amniotes are situated posterolaterally to the parietals. The position of the tabulars on the skull roof and their relationships to other skull bones are quite variable (LEE 1997), but they can be identified by their contact to the medial occipital region, the cartilaginous structure that ossifies as the supraoccipital. This criterion is adopted from SPENCER (1994), who employed it to distinguish the tabular from the supratemporal, if the two bones are present in a position lateral to the parietal. None of the positional criteria argues against an identification of the supernumerary bone as a tabular.

(d) Neomorphic ossification. Cranial ossifications that cannot be homologised with traditional skull elements are not uncommon among archosaurs. Well-known examples of elements otherwise unknown in amniotes included the predentary bone of ornithischian dinosaurs, and the rostral bone of ceratopsians. A second possibility is that dermal ossifications (osteoderms) might have been secondarily incorporated into the skull, and thus give the appearance of newly evolved or supernumerary elements. This process has been suggested among crurotarsans for the palpebral of some crocodiles (IORDANSKY 1973), and for one (to three) palpebrals in ornithischian dinosaurs and pterosaurs (COOMBS 1972).

The homology of the supernumerary bone with the epiotic or the postparietal can be dismissed on positional grounds. This leaves the tabular and a neomorphic ossification as the most likely identification based on topographical evidence.

The observation that secondarily incorporated osteoderms often are not firmly attached to, but superficially overlie the original cranial elements, has been suggested as a criterion to identify such elements (LEE 1997). The firm integration of the supernumerary element in the parieto-squamosal bar of both *Smilosuchus gregorii* and *Mystriosuchus* species B might disfavour such an interpretation. However, the criterion does not necessarily apply to "true" neomorphic ossifications, and the evolution of incorporated osteoderms may well lead to bones fully integrated in the skull (e.g. in ankylosaurian and pachycephalosaurian dinosaurs, COOMBS & MARYANSKA 1990; MARYANSKA 1990).

The presence of a tabular is incongruent with the generally accepted phylogenetic position of phytosaurs as the most basal clade of crurotarsan archosaurs. Recent reconstructions of amniote phylogeny unequivocally suggest that the tabular was lost in an early stage of diapsid evolution well before the split of Archosauromorpha and Lepidosauria, although the loss perhaps occurred several times independently (LAURIN & REISZ 1995; DEBRAGA & RIEPPEL 1997; LEE 1997). According to our knowledge, there is definitely no phylogenetic continuity among archosaurs to retain this element, and it seems anachronistic to find a tabular in a crurotarsan. This is a strong argument against an interpretation of this element as a tabular, however, there is still the possibility that a reversal has taken place in phytosaurs.

Other criteria such as parsimony cannot resolve the problem of homology of the bone in question: both the reappearance of a previously lost skull bone and the introduction of a neomorphic element requires one evolutionary step. In the absence of further evidence, it remains thus unresolved whether the ossification represents a tabular in accordance with CAMP's (1930) identification, or a neomorphic ossification probably unique to phytosaurs. For this reason, the neutral term supernumerary occipital element is chosen here. Regardless of the identification, the findings nevertheless support CAMP's

conclusion that the supernumerary bone of phytosaurs fuses to the parietal during ontogeny. The structural differences of these elements between *Smilosuchus gregorii* and *Mystriosuchus* species B suggest, considering the size of GPIT 261/001, a prolonged individuality of the element in this specimen. The Trossingen skull perhaps exhibits a trait in this species differing from the majority of phytosaurs in the retention of this bone as an individual element. This would be in accord with other features that suggest a persistence of "juvenile" characters in this specimen, such as the discrete orbitosphenoid and the persisting exoccipital-opisthotic suture on the paroccipital process. Similarly, CAMP (1930: 98) noted that his "tabulars" only occasionally maintain their identity in mature individuals. However, this cannot be decided in absence of developmental evidence, and the presence of the ossification may also represent an individual variation.

3.3.3.4 Presphenoid

CAMP (1930) was the first author to describe an unpaired presphenoid bone in *Smilosuchus gregorii*, situated between the parasphenoid, basisphenoid, the prootics, and the laterosphenoids above the hypophyseal fossa, and bordering the foramen opticum ventrally. Later, he confirmed the individuality of the bone in a specimen of *Machaeroprosopous zunii* (? *Leptosuchus adamanensis*, Long & Murry 1995) and corrected the outline of the bone shown in a previous reconstruction (CAMP 1942). A survey of the literature shows that in a number of braincase descriptions authors explicitly failed to identify a discrete ossification in the corresponding position (*Paleorhinus bransoni*: LEES 1907; *Brachysuchus*: CASE 1929, but see part 3.3.3.5; *Leptosuchus crosbiensis*: CASE & WHITE 1934; *Smilosuchus*: COLBERT 1947). The absence of a presphenoid in numerous taxa including GPIT 261/001 raises the question, whether such an element is restricted to an ingroup of Phytosauria or whether it is even present at all in phytosaurs. This area of the braincase has usually been referred to the basisphenoid, i.e. the clinoid process of the bone. Also, for the remaining and apparently well established occurrences of a presphenoid, the evidence seems to be not fully conclusive in "*Parasuchus hislopi*" (D. GOWER, pers. comm., 1997). This leaves *Smilosuchus gregorii* (the type only, COLBERT 1947) and *Leptosuchus adamanensis* the only taxa at present in which a separate presphenoid ossification has been demonstrated with certainty so far.

3.3.3.5 The position of the prootic foramen

In *Mystriosuchus* and *Smilosuchus* (CAMP 1930), the external opening of the prootic foramen, the exit of the trigeminal nerve and the medial cerebral vein, is surrounded entirely by the prootic. The laterosphenoid is also excluded from the prootic foramen in *Angistorhinopsis*, but in this form the clinoid process of the basisphenoid reaches the foramen ventrally (HUENE 1922). In a neurocranial reconstruction of *Brachysuchus*, CASE (1929) extends the basisphenoid along the anterior rim of the prootic foramen further dorsally up to the foramen of the nervus opticus. This is such a peculiar condition that it is not considered here until further re-examination is possible, especially as the same author later questioned his interpretation, though, without presenting an alternative (CASE & WHITE 1934). This is all in contrast to non-phytosaurid phytosaurs or, more precisely, to "*Parasuchus hislopi*", in which the laterosphenoid participates in the border of the foramen (CHATTERJEE 1978).

Smilosuchus and *Mystriosuchus* follow the plesiomorphic pattern for Archosauria regarding the boundary of the prootic foramen. The participation of the laterosphenoid has only been described in the basal archosaur *Shansisuchus* (GOWER & SENNIKOV 1996), and was suggested as an autapomorphy of this species. For the same reason, the character state differentiates "*Parasuchus hislopi*" from other phytosaurs.

3.3.4 The diagnostic characters of *Mystriosuchus* species B

In this section, the characters identified as diagnostic for *Mystriosuchus* species B, and characters distinguishing this species from *Mystriosuchus planirostris*, are listed and discussed. For convenience, the complementary state of each character state pair is given in parenthesis.

3.3.4.1 Diagnostic characters

(1) alveolar ridges much more prominent in anterior part of premaxillae, and semi-circular in cross-section; [convexity of alveolar ridges distinctly flattened].

In *Mystriosuchus planirostris*, the alveolar ridges form longitudinal, convex structures, which are distinctly flattened on the ventral side (RENESTO & PAGANONI 1998: fig. 1B) and correspond to the shape of alveolar ridges in other slender-snouted phytosaurs.

(2) parietal process of the squamosal extends far onto the supraoccipital shelf, and participates in forming the descending lamina of the parietal-supraoccipital complex; [parietal process restricted to horizontal part of the parieto-squamosal bar].

In all phytosaurs with depressed parieto-squamosal bars including *Mystriosuchus planirostris*, the dorsal aspect of the parietal process of the squamosal is limited to the lateral half of the bar. The squamosal may nevertheless extend far medially below the parietal/supernumerary occipital bone complex (e.g. *Smilosuchus*, CAMP 1930). GPIT 261/001 is the only specimen in which the squamosal actually takes part in forming the sharp, either sloping or vertical lamina of the parieto-squamosal bar.

(3) lamina of the parietal process of the squamosal lies on the anterior face of the paroccipital process and contacts the prootic anteromedially; [lamina absent, or lamina does not meet the prootic].

Although *Nicrosaurus kapffi* SMNS 4378 shows a similar lamina of the squamosal (Fig. 2.7), *Mystriosuchus* species B is the only phytosaur taxon in which the squamosal is known to greatly overlap the opisthotic and make contact with the prootic. The character state is unknown for the majority of phytosaur taxa including *Mystriosuchus planirostris*, and is therefore only tentatively suggested as diagnostic for *Mystriosuchus* species B.

(4) lobate extension on the vertical rim of the squamosal processes of the parietal; [vertical rim of the squamosal processes straight].

Such lobes are not present in the specimens of *Mystriosuchus planirostris*, and have not been reported or figured for other phytosaur taxa with rounded parietal-supraoccipital complexes such as *Pseudopalatus pristinus* and *Arribasuchus buceros*.

(5) posttemporal fenestra reduced to a narrow slit; [posttemporal fenestra oval].

The posttemporal fenestra of the Trossingen skull is as wide as in *Mystriosuchus planirostris*, but in the type species the shape of the opening is still plesiomorphically oval, lying in the wide and relatively deep recess formed by the overhang of the parieto-squamosal bar over the paroccipital process (e.g. SMNS 13240). In *Mystriosuchus* species B, the medial parts of the parieto-squamosal bar and the paroccipital process have merged to a morphologically indistinguishable strut in occipital view, although the edge of the parieto-squamosal bar is still marked when seen from anterior. The posttemporal fenestra is reduced to a mere slit, and it is doubtful whether the opening might have still served as a passage for the vena capitis dorsalis. Therefore, *Mystriosuchus* species B shows the most derived state among Phytosauria.

3.3.4.2 Characters distinguishing *Mystriosuchus* species B from *Mystriosuchus planirostris*

The following characters are differently developed in both species of *Mystriosuchus*, and are may therefore be used to distinguish both taxa, but are not regarded as diagnostic for various reasons. Characters (2) and (4) are the complementary states of the diagnostic characters of *Mystriosuchus planirostris*. Characters (3), and (11) - (12) are still problematic. Regarding character (1), (5) - (8), and (13), no character state can be suggested as diagnostic for one of both species as long as a phylogenetic framework has not been established, because the polarity of the character transformation depends on the phylogenetic position of the genus *Mystriosuchus*. For example, advocating a sistergroup relationship *Paleorhinus* + *Mystriosuchus* (LONG & MURRY 1995) results in the consequence that character (7), presence of a short posterior process of the squamosal, is autapomorphic for *Mystriosuchus planirostris*, while *Mystriosuchus* species B retained the plesiomorphic state. The same character state interpreted in the framework of the sistergroup *Mystriosuchus* + *Pseudopalatus* (BALLEW 1989) means that the presence of a short process is plesiomorphic within the genus, and the complete lack of such a the process in *Mystriosuchus* species B necessarily a more derived condition.

(1) massive rostrum (GREGORY & WESTPHAL 1969; HUNT & LUCAS 1989b); [*Mystriosuchus planirostris*: rostrum elongated and slender].

The length of the rostrum in *Mystriosuchus* species B is only 8 times the width at the premaxilla/maxilla contact, in contrast to 14 times in *Mystriosuchus planirostris*.

(2) prenarial length equals two times the narial + postnarial skull length (LONG & MURRY 1995); [*Mystriosuchus planirostris*: prenarial length equals three times the postnarial length].

Since the greatly elongated rostrum is interpreted as a derived diagnostic character of *Mystriosuchus planirostris*, the less elongated snout of *Mystriosuchus* species B is only a distinguishing feature between these species.

(3) presence of a premaxillary crest; [*Mystriosuchus planirostris*: absent].

It is very tempting to propose such a conspicuous and clearly derived character, the premaxillary crest, as an autapomorphy of *Mystriosuchus* species B. However, the findings in *Nicrosaurus* species B (part 2.3.3.2) may serve as a warning not to base phytosaur species on snout crest characters as long as a uniform character distribution is

not supported by a reasonable number of specimens. Moreover, there are indications that a premaxillary crest may also occur in *Mystriosuchus planirostris*: firstly, the skull SMNS 11126(2), now lost, but figured in HUENE (1911: fig. 17), showed a short, but very distinctive premaxilla elevation on the anterior part of the snout. However, there are difficulties with the specific assignment of this skull. A second possible specimen is represented by the fragment of an anterior right premaxilla GPIT 2088.002. According to the provenance from the Aixheim region this possibly belongs to *Mystriosuchus planirostris*, although the incompleteness of the specimen does not allow identification other than as a slender-snouted phytosaur. The tip of the premaxilla above the fangs is elevated into a 50 mm long, narrow, and anteroposteriorly asymmetric crest, showing a steep anterior edge and more gently sloping posterior rim. In both these specimens, the premaxillary crest was, or is, proportionally much shorter than in *Mystriosuchus* species B and lies at or almost immediately behind the tip of the snout. Finally, there is SMNS uncat. no. 11 (probably *Nicrosaurus* species B), which also shows a premaxillary crest, although it is different in shape and length to that of the aforementioned specimens.

In conclusion, for the first time in a phytosaur the presence of a "natural" premaxillary crest has been demonstrated in *Mystriosuchus* species B, but there are indications that a similar structure was present in other closely related European taxa. The taxonomic and phylogenetic value of the presence of a premaxillary crest is doubtful. The premaxillary crests differ in shape, length, and position, but with our present knowledge about character distribution and intraspecific variability it seems unwise to use these differences for taxonomic purposes.

(4) less abrupt contour between naris and rostrum (GREGORY & WESTPHAL 1969; HUNT & LUCAS 1989b); [*Mystriosuchus planirostris*: steep prenarial slope].

The prenarial area of the Trossingen skull slopes more gently and retains the more or less transversely convex outline seen in the majority of crest-less phytosaurs. According to less derived phytosaurs (non-phytosaurid phytosaurs, Angistorhininae, *Rutiodon carolinensis*, *Nicrosaurus* species B) and *Mystriosuchus planirostris*, this is the primitive character state.

(5) quadrate foramen somewhat smaller and situated in a triangular recess; [*Mystriosuchus planirostris*: larger, and placed in a round recess].

The shape of the quadrate foramen is similar to that in the majority of phytosaurs, and therefore probably represents a plesiomorphically retained feature.

(6) posterior extremity of squamosal blunt; [*Mystriosuchus planirostris*: pointed or knob-like extension].

(7) posterior process of squamosal lacking, the bone terminates above the paroccipital process of the opisthotic and in front of the posterior extremity of the quadrate; [*Mystriosuchus planirostris*: short posterior process that usually overhangs the quadrate].

(8) paroccipital process is the posteriormost projection of the squamosal; [*Mystriosuchus planirostris*: posterior process of the squamosal is the posteriormost point of the skull].

As the same condition occurs in "*Parasuchus*" (CHATTERJEE 1978) and *Brachysuchus* (CASE 1929: fig. 7), this character state is probably primitive. It is of limited significance for distinguishing both species of *Mystriosuchus*, since the same condition is also present in at least one specimen of *Mystriosuchus planirostris* (SMNS uncat. no. 184).

(9) supraoccipital reaches posttemporal fenestra and borders its dorsomedial half; [*Mystriosuchus planirostris*: supraoccipital excluded from posttemporal fenestra].

(10) exoccipitals unite basally and exclude basioccipital from floor of the foramen magnum; [*Mystriosuchus planirostris*: basioccipital reaches foramen magnum].

This character state distinguishes *Mystriosuchus* B from *Mystriosuchus planirostris*, as far as can be determined in the specimens. This character was employed in basal archosaur phylogeny and is further discussed in GOWER & SENNIKOV (1996), who considered this state as apomorphic. *Mystriosuchus*, and thus Phytosauria, seem to be polymorphic regarding the character. It is unknown whether in *Mystriosuchus planirostris* the exoccipitals remain separate (coded 0 in GOWER & SENNIKOV 1996) or converge to meet finally on the floor of the braincase (coded 2).

(11) separate ossification (orbitosphenoid) anterior to laterosphenoid; [*Mystriosuchus planirostris*: no evidence].

Pending further investigation of *Mystriosucvhus planirostris*, the presence of a discrete orbitosphenoid might be autapomorphic for *Mystriosuchus* species B. Because of the uncertainties discussed above, this character is only tentatively included.

(12) additional paired elements posterolateral to the parietals (homologous with CAMP's 1930 tabulars); [*Mystriosuchus planirostris*: absent].

Character states involving the fusion of distinct elements are always difficult to interpret taxonomically and phylogenetically, as long as it is impossible to demonstrate that the fusion is not a consistent ontogenetic trait. This character also remains problematic because of the uncertainty concerning the homology of the supernumerary bone and whether its presence is subject to individual variation. The supernumerary bone must be confirmed in more specimens before it may be ranked as a convincing diagnostic character.

(13) dentition closely spaced, and size-differentiated, and the anterior premaxilla and [posterior] maxilla bear enlarged teeth; maxilla with convex ventral margin (LONG & MURRY 1995); [*Mystriosuchus planirostris*: premaxillary and anterior maxillary teeth wide-spaced, teeth of similar size, maxillary rim straight].

The description by LONG & MURRY (1995) is correct for the (anteriormost) premaxillary teeth, however, enlarged fangs are plesiomorphic within Phytosauria. The anteriormost two premaxillary teeth of GPIT 261/001 are clearly more hypertrophied than in *Mystriosuchus planirostris*, and may represent a character that distinguishes between these two species.

The convex outline of the maxilla is usually correlated with larger (and highly differentiated) posterior maxilla teeth. This feature thus seems to be related to the nature of the dentition, which, in combination with the larger alveoli in the posterior maxilla, supports the interpretation of differentiated maxilla teeth.

3.3.4.3 Characters rejected as non-diagnostic, or incorrectly identified character states

(i) rostrum sculptured (LONG & MURRY 1995).

The character description is incorrect. The rostrum of GPIT 261/001 (here in the definition of the prenarial part of the skull) is unsculptured, and sculpture on the part of the snout in front of the orbits does not differ significantly between the two species of *Mystriosuchus*.

(ii) naris depressed well below skull table (HUNT & LUCAS 1989b).

As correctly stated by LONG & MURRY (1995), there is no substantial difference between both species of *Mystriosuchus* regarding the elevation of the external nasal openings (Figs 3.1; 3.4).

(iii) relative length of naris (LONG & MURRY 1995).

According to the authors, the naris of GPIT 261/001 occupies the space above the anterior two thirds of the antorbital fenestra, rather than above the anterior half as is suggested to be typical for *Mystriosuchus planirostris*. The length of the naris relative to the antorbital fenestra as suggested by LONG & MURRY (1995) only applies to some specimens of *Mystriosuchus planirostris*: the same condition as in *Mystriosuchus* species B seems to be present in SMNS 10260 and HMB MB.I.008.05. Moreover, I found it very difficult, or even impossible to distinguish exactly between both the character states.

(iv) less well rounded antorbital fenestra (HUNT & LUCAS 1989b).

The antorbital fenestra of GPIT 261/001 is somewhat dorsolaterally compressed especially in its middle section, which results in a narrower and "kinked" opening (Fig. 3.4) than the shape reconstructed by MCGREGOR (1906) for *Mystriosuchus planirostris* (Fig. 3.1). However, the outline actually falls well within the variation of fenestral shapes seen in *Mystriosuchus planirostris*, being paralleled, for instance, by specimens SMNS uncat. no. 184 and 185.

(v) jugal excluded from antorbital fenestra (HUNT & LUCAS 1989b).

The identification of the character state, suggested by these authors on the basis of HUENE (1911), is correct (Fig. 3.4). However, regarding the configuration of the skull elements around the antorbital fenestra, intraspecific variability has been demonstrated for *Nicrosaurus kapffi* (part 2.2.5.2). It is reasonable to assume that the jugal not participating in the border of the antorbital fenestra is subject to individual variation in other phytosaur species as well.

(vi) paroccipital process of opisthotic strongly produced laterally (LONG & MURRY 1995).

It has been shown above that in phytosaurs the relative width of the paroccipital process depends on the width-to-height relationship of the postorbital part of the skull (part 2.2.5.3). The relative width of the skull in occipital view (and thus that of the paroccipital process) of the Trossingen skull as expressed by the width-to-height index of 2 is somewhat greater than the average figure for *Mystriosuchus planirostris* (1.75). However, the difference is far less than the degree of intraspecific variation seen in *Nicrosaurus kapffi* (Tab. 2.2.2), and is thus probably insignificant. There are no other character states of the paroccipital process in *Mystriosuchus* species B such as anteroposterior thickness, orientation of the posterior surface, shape of the ventral

opisthotic ridge, or prominence of the posteromedian ridge that do not lie within the range of variability seen in *Mystriosuchus planirostris*.

Chapter 4

Nomina dubia and *Nomina nuda*

Section 4.1

Phytosaurus cylindricodon JAEGER, 1828 [*nomen dubium*] and *Phytosaurus cubicodon* JAEGER, 1828 [*nomen dubium*]

4.1.1 Systematic palaeontology

Archosauria COPE, 1869

Crurotarsi SERENO et ARCUCCI, 1990

Phytosauria JAEGER, 1828 (*sensu* DOYLE & SUES 1995)

Type genus: *Phytosaurus* JAEGER, 1828

Genus *Phytosaurus* JAEGER, 1828

Synonyms:

Cylindricodon JAEGER, 1828

Cubicodon JAEGER, 1828

Type species: *Phytosaurus cylindricodon* JAEGER, 1828

Synonym: *Phytosaurus cubicodon* JAEGER, 1828

Holotype: Since the remains arguably belong to a single individual (PLIENINGER in MEYER & PLIENINGER 1844; WESTPHAL 1963a), all syntypes represent the holotype,

and *Phytosaurus cylindricodon* has priority over *Phytosaurus cubicodon* because of page priority. The list gives the description of the fragments and their current repository:

GPIT uncat. no. 402a, mould of the lower jaw symphysis, posterior part, most of the left mandible is missing [JAEGER 1828: pl. 6 fig. 3 part "A-A"; the alveolus pl. 6 fig. 7 was later inserted in tooth position 7, and an unfigured alveolus from the material in position 12].

GPIT uncat. no 402b, steinkern of an anterior tooth [JAEGER 1828: pl. 6 figs. 9-11].

GPIT uncat. no. 402c, steinkern of an alveolus, *cylindricodon*-type [JAEGER 1828: pl. 6 fig. 6].

GPIT uncat. no. 402d, steinkern of Meckel's cartilage [JAEGER 1828: pl. 6 fig. 16].

GPIT uncat. no. 402e, steinkern of four alveoli, syntype of *Phytosaurus cubicodon* [JAEGER 1828: pl. 6 figs. 18 and 20].

SMNS uncat. no. 402f, mould of the lower jaw symphysis, anterior part [JAEGER 1828: pl. 6 fig. 3 part "B", anterior left part "D-D-C" is missing].

SMNS uncat. no. 402g, moulds of four large bicarinate teeth [JAEGER 1828: pl. 6 figs. 12-15].

SMNS uncat. no. 402h, steinkerns of three alveoli, *cylindricodon*-type [JAEGER 1828: pl. 6 figs. 4-5].

SMNS uncat. no. 402i, anterior tooth [JAEGER 1828: pl. 6 fig. 8].

SMNS uncat. no. 402j, steinkern of four alveoli, syntype of *Phytosaurus cubicodon* [JAEGER 1828: pl. 6 figs. 17 and 19].

Type locality: Rübgarten near Tübingen (Fig. 1.1; for details see Appendix C, 8).

Type horizon: Most likely middle Stubensandstein (see Appendix C, 8).

Referred specimens: None.

Distribution: Restricted to type locality.

Stratigraphic range: Restricted to type horizon.

Age: Lower (or Middle) Norian.

4.1.2 Discussion

The nomen *Phytosaurus cylindricodon* was originally erected as "genera or species" (JAEGER 1828: 22; he left the issue undecided, see quotation in subsection 2.1.1) *Cylindricodon* and *Cubicodon* of the family "Phytosaurus" (JAEGER 1828: 44; also JAEGER 1844), a pattern similar to the more famous (and at the time of JAEGER's publication still species-less) genera *Megalosaurus* BUCKLAND, 1824 and *Iguanodon* MANTELL, 1825. The name is based on a fragmentary lower jaw, which is in most parts preserved as a natural mould. In contrast to a notion in BALLEW (1989), there is no evidence of a partial skull having been recovered.

The find of such strange reptilian remains from strata which were previously thought to be barren of fossils received much attention among contemporary scholars. Most of the attention was in form of justified doubt about JAEGER's preservational and anatomical interpretation of the specimens, and alternative identifications such as a man-made artefact, a natural but inorganic phenomenon, a pycnodontid fish, or a temnospondyl amphibian were soon put forward (MEYER 1847-55). QUENSTEDT (1843) was the first to identify the true nature of the teeth as steinkerns, and his observation was fully vindicated by the study of MEYER & PLIENINGER (1844), and soon became generally accepted.

It is often stated that JAEGER mistook *Phytosaurus* for a body fossil - not exactly the best recommendation for a practising physician and a then well established savant of natural history. This is only partially correct. Actually, JAEGER (1828) did realise that the "teeth", referred by him to an upper jaw of *Phytosaurus cylindricodon*, consisted of the same, but more fine-grained, substance as the surrounding matrix (p. 27, 28). However, he interpreted them as completely remineralised teeth or sedimentary fillings of the pulp cavity, which after subsequent diagenetic loss of dentine and enameloid copied the original morphology of the tooth. He also assumed that bone tissue had partially vanished (p. 25) and was partially substituted by sediment (p. 29), and finally concluded that *Phytosaurus cylindricodon* is a reptile with an acrodont ankylosed dentition like a monitor lizard, but very peculiar tooth morphology. He also identified correctly the presence of thecodont, pointed, and bicarinate teeth in the dentition (contra BALLEW 1989: 325), which he referred to the lower jaw of the animal comparable to the tusk-like canines of a boar (p. 30). It is not literally stated, but it can be deduced from the quotation "the nature of the [tooth] surface shows much similarity with *Cylindricodon*" (p. 34), that he assumed the same mode of preservation for the steinkerns of *Phytosaurus cubicodon*. Finally, *Phytosaurus cylindricodon* and *cubicodon* were not only distinguished on the

basis of their morphology alone, but also by the alleged mode of attachment (acrodont in *Cylindricodon*, pleurodont in *Cubicodon*).

The majority of the fragments figured on JAEGER's original plate 6 were reproduced and made available to a broader audience by HUENE (1911: fig. 24). Although numerous authors expressed their doubts about the validity of the name, HUENE (1911) and WESTPHAL (1963b) presented the only reviews so far, which deal with the issues of identification and synonymy in detail and are not confined to the oversimplified statement that *Phytosaurus* is poorly preserved and thus a dubious name. HUENE (1911) correctly points out that a number of characters, including the length of the symphysis (280 mm), the narrowing of the mandible from 66 mm at the end of the symphysis to about half the amount at the constriction behind the tip, the considerable expansion of the tip, the tight-spaced alveoli, the marked size decrease of the alveoli from posterior (*Phytosaurus cubicodon*) to anterior (*Phytosaurus cylindricodon*), an alveolus suggesting a very large fang, and direct evidence for large, triangular posterior teeth (JAEGER 1828: pl. 6 figs. 14-16), can be determined in the type material. The validity of *Phytosaurus* cannot simply be denied on the grounds of poor preservation. On the base of the then available knowledge, HUENE made a convincing case for synonymising *Nicrosaurus kapffi* with *Phytosaurus cylindricodon*. WESTPHAL (1963b) discussed and rejected the nature of the alveolar spacing, the form of alveoli, and the angle between splenial and dentary as diagnostic characters for reasons of ontogenetic and individual variation among phytosaurs. Even if these characters are not considered, the remaining characters still effectively exclude *Nicrosaurus* species B and *Mystriosuchus planirostris*, but are fully consistent with *Nicrosaurus kapffi*. In the last decades, the type locality was usually referred to the upper Stubensandstein (BRENNER 1973; BENTON & WILD 1993). This meant that *Phytosaurus cylindricodon* was the only phytosaurian find known from this youngest unit of the Stubensandstein in Southwest Germany, arguing against any synonymy on stratigraphic grounds. It is much more likely, however, that the type is derived from middle Stubensandstein (see Appendix C, 8) and *Phytosaurus* is actually contemporaneous with *Mystriosuchus* and *Nicrosaurus*.

However, the binomen *Phytosaurus cylindricodon* is correctly accepted as a *nomen dubium* by recent workers (BALLEW 1989; LONG & MURRY 1995). The character states pointed out by HUENE (1911) apply to every heterodont phytosaur, not only to *Nicrosaurus kapffi* in particular. Nothing argues against the synonymy of *Phytosaurus cylindricodon* with the fourth species present in the Norian of Germany, *Mystriosuchus* species B. It is shown in this study (section 3.3), that there is clear evidence of *Mystriosuchus* species B having a robust snout, a tight-spaced tooth pattern, and some

indications are present for a heterodont dentition. Furthermore, it is the type of a species (and generotype) that should provide the character states to base a taxon upon and form the foundation to refer additional specimens, not the other way round.

The invalidity of *Phytosaurus cylindricodon* does not prevent *Phytosaurus* being the type genus of the family Phytosauridae JAEGER, 1828 (Art. 61(a) ICZN).

Section 4.2

Belodon plieningeri MEYER, 1844 [*nomen dubium*]

Systematic palaeontology

Archosauria COPE, 1869

Crurotarsi SERENO et ARCUCCI, 1990

Phytosauria JAEGER, 1828 (*sensu* DOYLE & SUES 1995)

Genus *Belodon* MEYER, 1844

Type species: *Belodon plieningeri* MEYER, 1844

Syntypes:

Mandible fragment including one tooth (MEYER & PLIENINGER 1844: 43, pl. 12 figs. 21-22; MEYER 1847-55: pl. 20 fig. 2). Current repository unknown.

Isolated tooth lacking most of the root (MEYER & PLIENINGER 1844: 43, pl. 12 fig. 20; MEYER 1847-55: pl. 20 fig. 3). Current repository unknown.

Type locality: Löwenstein, northern Württemberg (Fig. 1.1); locality details unknown (see Appendix C, 1.2).

Type horizon: Stubensandstein; stratigraphic details unknown (see Appendix C, 1.2).

Referred specimens: None.

Distribution: Restricted to type locality.

Stratigraphic range: Restricted to type horizon.

Age: Lower (or Middle) Norian.

Discussion

Belodon plieningeri was the second phytosaur genus and species to be named. The name first appears in a preliminary note in MEYER (1842) outlining the taxonomy of temnospondyls and reptiles he obtained from the Keuper of Württemberg to be published two years later in cooperation with PLIENINGER. The diagnosis includes the literal translation of the genus name only ("arrow-shaped morphology") and no reference to particular specimens is made; hence the binomen as erected in 1842 must be regarded as a *nomen nudum*. The name became formally available with the detailed description by MEYER (in MEYER & PLIENINGER 1844: 43-44). Both syntypes were illustrated on plate 12 (figs. 21-22 and fig. 20). MEYER (1847-55: 148) gave a summary characterisation and, apparently unhappy with the poor quality of the previous illustrations, provided his own drawings of the type material (pl. 20 figs. 2 and 3). Since the syntypes are lost (details see Appendix C, 1.1.1), these illustrations must form the basis for the taxonomic assessment of *Belodon plieningeri*.

The specimen illustrated by MEYER & PLIENINGER (1844: pl. 12 figs. 21-22) is the fragmented posterior part of a right mandible, including parts of the splenial and the dentary plus the splint-like anterior process of the surangular that participates in forming the lateral alveolar border (similar to *Nicrosaurus kapffi*, subsection 2.2.4, and *Nicrosaurus* species B, HUENE 1911: 27). The tooth, which is preserved transversely split *in situ* in the fragment, corresponds essentially with the morphology of the isolated second syntype (MEYER & PLIENINGER 1844: pl. 12 fig. 20), and differs mainly in its tooth crown height being greater (c. 25 mm, in contrast to c. 17 mm). Both teeth are bilaterally asymmetrical with the labial side more vaulted than the lingual, bicarinate, and with a non-recurved tooth axis. They lack well developed mesial and distal blade-like flanges, and only the apical parts of the carinae have been described as showing minute serrations.

The majority of teeth of *Mystriosuchus planirostris* are fundamentally different from those forming the basis of *Belodon plieningeri*. The triangular bicarinate teeth

occurring in posteriormost positions are much smaller than the *Belodon* syntypes (see subsection 3.2.2). It is unknown whether *Mystriosuchus* species B had any asymmetrical and carinate blade-like teeth (see subsection 3.3.2).

The dentition of *Nicrosaurus* species B is only partially known. The basic tooth type represented by *Belodon plieningeri* occurs in the posteriormost maxilla and dentary. However, in *Nicrosaurus* species B such teeth are considerably smaller than in *Belodon plieningeri*: they reach at best half the size to the tooth figured in MEYER & PLIENINGER (1844: pl. 12 figs. 21-22), even in the largest specimens known (SMNS 4059, MEYER 1861: pl. 29 fig. 5; GPIT 2070.001, pers. obs.; mandible: MEYER 1865: pl. 23). Furthermore, the tips of posterior maxillary teeth in *Nicrosaurus* species B are somewhat elongated and set off from the carinae (MEYER 1865: pl. 23 fig. 1). This is not the case in the isolated syntype tooth of *Belodon plieningeri*.

Provided the tooth morphology of *Nicrosaurus kapffi* is typical for strongly heterodont phytosaurs, such animals show a marked heterodont dentition: large fangs are situated in the tips of the snout and the mandible. There is an array of premaxillary teeth grading anteroposteriorly from undifferentiated conical teeth into high, slender, and strongly asymmetrical tooth shapes. The maxilla and dentary teeth similarly grade from an unspecialised conical shape into the triangular, bicarinate tooth morphology with laterally compressed, extensive flanges, which are usually regarded as typical for heterodont phytosaur taxa. Teeth showing the combination of all characters of the types of *Belodon plieningeri* are not included in the dentition of the anterior dentary and the whole premaxilla dentition of *Nicrosaurus kapffi*. The tooth morphology of *Belodon plieningeri*, however, occurs consistently either in the middle section of the maxilla or the posterior part of the dentary. The posteriormost maxilla teeth in such strongly heterodont morphotypes can be distinguished by a recurved tip overhanging the distal rim of the tooth root and extensive development of blades. Furthermore, the carinae of posterior maxilla as well as the posteriormost dentary teeth are usually fully serrated.

In conclusion, the syntypes *Belodon plieningeri* definitely represent a phytosaur. The syntype specimens match teeth that occur in certain positions (mid-section of the maxilla; posterior part of the mandible) of strongly heterodont phytosaurs. However, it is not possible at present to identify phytosaur species based on characters of isolated teeth - in general because the intra- and interspecific variation of phytosaur dentitions and thus the consistency of character states at species level is poorly known. In the case of *Belodon plieningeri*, the type series is not available, and unique (i.e. potentially autapomorph) characters have not been noted in the original description. Therefore, *Belodon plieningeri* is correctly identified as a *nomen dubium* in the most recent literature (BALLEW 1989; HUNT & LUCAS 1989b; LONG & MURRY 1995). For a long time, the

skulls referred here to an unnamed species of *Nicrosaurus* have been regarded as the actual animal pertaining to the tooth taxon *Belodon plieningeri* (see synonymy list for *Nicrosaurus* species B, subsection 2.3.1). It is important to note that a synonymy of both taxa is unlikely on the basis of detailed tooth morphology and, more important, the size difference. *Belodon plieningeri* might rather be a subjective senior synonym of *Nicrosaurus kapffi*. It is not justified by evidence to transfer the binomen *Belodon plieningeri* to the slender-snouted species of *Nicrosaurus* as formerly practised by MEYER (1860a, 1861), GREGORY (1962), WESTPHAL (1963b) and GREGORY & WESTPHAL (1969).

Section 4.3

Belodon ingens E. FRAAS, 1896 [*nomen nudum*] (= *Belodon giganteus* E. FRAAS ms. [*nomen nudum*])

The type specimen of *Belodon ingens* was acquired by the SMNS as early as (?) May 1896 (acquisition record, SMNS archives) from Mr. HAUG, a teacher representing a local naturalists' society from the vicinity of Aixheim, the Naturhistorischer Verein Spaichingen. This marked the beginning of a fruitful relationship that gained the museum a number of fine *Mystriosuchus* specimens. The specimen in question is registered as "Unterkief." [lower jaw] SMNS 9439 in the inventory catalogue, with the remark that is was derived from the Aixheim region. FRAAS apparently could not resist adding the manuscript name "*Belodon giganteus* Fr." to the entry in the catalogue.

However, FRAAS must have changed his mind soon later, because he finally named a new species *Belodon ingens* based on this specimen the same year (FRAAS 1896). The naming was clearly intended as preliminary note and incorporated in FRAAS' overview on Triassic amphibians and reptiles from Southwest Germany. The specimen was not even fully prepared at the time of publication. Consequently, no figure was presented, and the description comprises a brief and uninformative paragraph, stating that the new species is characterised by (1) "the considerable length [of the mandible] of 1 m" and (2) "by the strong dentition, showing much resemblance to *B. Kapffii* [sic], but also differences" (FRAAS 1896: 15; my translation). Unfortunately, a full description was never published. The type specimen of *Belodon ingens* is not traceable in the SMNS any more. It is impossible to designate a neotype on the basis of the poor anatomical

information presented by FRAAS. Since the taxon was inadequately diagnosed in the first place, *Belodon ingens* is considered here a *nomen nudum*.

It is a strange coincidence that *Belodon ingens* is not described in MCGREGOR's (1906) monograph on the *Mystriosuchus* from Aixheim. FRAAS (1896) failed to mention explicitly that the species name is based on a lower jaw only, which resulted in MCGREGOR's (1906) misconception of *Belodon ingens* being represented by a large phytosaur skull. It is quite reasonable to assume that MCGREGOR never saw the type. The erroneous statement was subsequently adopted several times in the literature (MEHL 1913; CAMP 1930; WESTPHAL 1963b). Similarly, HUENE reviewed and redescribed in a series of papers (1902, 1907/08, 1909, 1911, 1922) virtually every important phytosaur specimen in Germany, but only mentioned *Belodon ingens* as synonym of *Nicrosaurus kapffi* in a list of species provided in 1909. This leaves the possibility that the specimen has been given away before both researchers visited the Stuttgart collection and still exists elsewhere. Alternatively, the specimen could have been destroyed in the air raid on the museum in 1944 (R. WILD, SMNS, pers. comm., 1996).

Probably based on the criterion of size, HUENE (1922) suggested that *Belodon ingens* represents a jaw referable to a skull of the taxon represented by GPIT 261/001. For the same reason, WESTPHAL (1963b) also regarded the species *ingens* as a synonym of *Mystriosuchus* species B (in his taxonomic scheme together with *Nicrosaurus* species B under the name *Belodon plieningeri*). Although this seems not to be an unreasonable suggestion, any hypothesis about synonymy cannot be tested and it is futile to speculate further on the taxonomic affinities of *Belodon ingens*.

Chapter 5

Phylogenetic analysis

Section 5.1
The aims of the analysis

BALLEW (1989) published the first and so far only phylogenetic framework of phytosaur interrelationships which is based on a cladistic analysis using parsimony. The cladogram resulting from this analysis is illustrated in Figure 5.1. A competing phylogenetic hypothesis has been put forward by LONG & MURRY (1995). Their view is illustrated in Figure 5.2. LONG & MURRY did not strictly employ cladistic techniques such as the consequent decisions of the plesiomorphic or apomorphic nature of character states, and only the groups underlined in Figure 5.2 have been defined explicitly as monophyletic by shared derived characters. No cladistic analysis based on parsimony is presented. A cladogram was consequently reconstructed from the systematic hierarchy suggested by the authors.

The results of these phylogenetic studies illustrated in Figures 5.1 and 5.2 differ fundamentally in the relationships of the genus *Mystriosuchus*. BALLEW (1989) argues for a sistergroup relationship of *Mystriosuchus* with *Pseudopalatus pristinus* based on several synapomorphies. By contrast, LONG & MURRY (1995) follow HUNT & LUCAS (1989b) in assuming a sistergroup *Mystriosuchus* + *Paleorhinus* (= Mystriosuchidae HUENE, 1915). In other words, in the first case *Mystriosuchus* forms the most derived phytosaur taxon representing the endpoint of a single lineage of forms in which the characters typical of "advanced" phytosaurs evolved successively. According to the second hypothesis, the genus is regarded as the closest relative of the most primitive phytosaurs that consequently must have acquired numerous identical features independently from other "advanced" phytosaurs. However, the study fails to support this assumption by presenting shared derived characters between *Mystriosuchus* and *Paleorhinus*, and does neither invalidate nor even discuss the significance of numerous

derived features that *Mystriosuchus* has in common with *Pseudopalatus* and *Arribasuchus*.

Both phylogenetic hypotheses have a number of points in common. In both studies, *Ebrachosuchus*, *Francosuchus*, "*Parasuchus*", and *Promystriosuchus* are treated as subjective synonyms of the genus *Paleorhinus*. *Paleorhinus* was identified and defined as a monophyletic taxon for the first time by BALLEW (1989). Likewise, LONG & MURRY (1995), after referring *Paleorhinus magnoculus* to their new genus *Arganarhinus*, grouped both genera in the subfamily Paleorhininae, which is not explicitly defined by synapomorphies, but subsequently treated as "quasi-monophyletic". In BALLEW (1989), *Paleorhinus* occupies the most basal position in the cladogram as a sistergroup to all other phytosaurs, the Phytosauridae *sensu* DOYLE & SUES (1995), or Paleorhininae is regarded as the higher taxon that includes all most primitive phytosaurs (LONG & MURRY 1995). Secondly, with exception of the discrepancy regarding *Mystriosuchus*, both cladograms show a consistent general tree topology. *Angistorhinus* (including *Brachysuchus*) is identified as most basal monophylum in the clade Phytosauridae (BALLEW 1989) or the family Rutiodontidae LONG et MURRY, 1995 (= Phytosauridae minus *Mystriosuchus*). Both studies identify an unresolved clade (*Rutiodon carolinensis* + *Leptosuchus* + *Smilosuchus gregorii*), which is either synonymised with the genus "*Rutiodon*" (BALLEW 1989) or grouped as the subfamily Rutiodontinae by LONG and MURRY, 1995. This clade forms the sistergroup of another clade comprising, in ascending order, *Nicrosaurus* + *Arribasuchus* + *Pseudopalatus* (= Pseudopalatinae of LONG & MURRY, 1995), or *Nicrosaurus* + *Pseudopalatus*, the latter being subdivided in the species (*Pseudopalatus mccauleyi* + (*Pseudopalatus buceros* + (*Pseudopalatus pristinus* + *Mystriosuchus planirostris*))) in BALLEW (1989). The close similarity of both competing phylogenetic hypotheses leads to the impression that a robust phylogenetic framework of phytosaur evolution has been established, and only the relationships of *Mystriosuchus* are still a subject of debate.

BALLEW's study is the first, and the so far only available, phylogenetic analysis of phytosaurs that employs cladistic methodology based on parsimony. However, there are several serious shortcomings with the analysis. Firstly, out of 64 characters used in her analysis 39 characterise the operational taxonomic units, and are hence uninformative regarding the resolution of ingroup relationships. As an additional five characters (numbered 49 - 53) are quoted in support of a clade that is not present in the cladogram, the phylogenetic hypothesis is effectively based on only 20 shared characters. Secondly, the results cannot be tested because neither a data matrix nor the settings of the parsimony analysis are given. More importantly, however, fundamental principles of the cladistic

method are violated: these include the acceptance of artificial groups, e.g. five synapomorphies are given for *Pseudopalatus buceros* (here: *Arribasuchus buceros*) + *Pseudopalatus pristinus*, although the "clade" is shown to be paraphyletic in the cladogram. Furthermore, DOYLE & SUES (1995) correctly pointed out that according to BALLEW's own analysis a number of putative aut- and synapomorphies of her OTUs (e.g. *Rutiodon carolinensis*) and clades (e.g. "*Rutiodon*", which includes the genera *Rutiodon*, *Leptosuchus*, and *Smilosuchus* in this study) are dubious or actually represent symplesiomorphic character states. BALLEW also frequently employed character combinations of plesiomorphic and apomorphic states as "synapomorphies" (characters 14 and 15, node E), a procedure that is methodologically incorrect and corresponds to a classic "non-A-group" definition (ELDREDGE & CRACRAFT 1980). Finally, the transliteration of the tree topology into a nomenclatural scheme is in parts incorrect in violating the principle of priority (article 23 ICZN): the genus-name *Mystriosuchus* E. FRAAS, 1896 has clearly seniority over *Pseudopalatus* MEHL, 1928. All these misinterpretations and the incorrect methodology raise *a priori* considerable doubts about the validity of the results of the analysis.

I do not wish to present and discuss a definite phylogenetic analysis of phytosaurs here. The primary information obtained from direct observation for such a purpose is far from sufficient, and the distribution of numerous characters taken from the literature are in need of scrutiny. However, there are two important taxonomic and phylogenetic questions I particularly wish to deal with at this stage:

(1) Does the evidence indeed support the hypothesis that the species referred to *Paleorhinus* or the taxa included in Paleorhininae form a monophylum as suggested by BALLEW (1989) and implied in LONG & MURRY (1995) and HUNT (1994), or do these taxa represent a paraphyletic assemblage that forms the stem group of Phytosauridae (CAMP 1930; GREGORY 1962a; WESTPHAL 1976; CHATTERJEE 1978)? This question must have important consequences for the nomenclature, i.e. the generic referral of the taxa involved, and for the assessment of the homology of a number of derived characters that evolved within Phytosauria.

(2) A solution of the dilemma where to place *Mystriosuchus* is certainly the most important decision that has to be made in phytosaur phylogeny, and the decision is crucial to our understanding of the evolution of some "typical" features of phytosaurs. It is unavoidable from the combination of apparently primitive with highly derived osteologic features in *Mystriosuchus* that a number of serious character conflicts arise. These

characters include features that have always been regarded as characteristic of derived phytosaurs, and some of them such as the nares located directly in front of the orbits, the depressed parieto-squamosal bar and the presence of an elongated posterior process of the squamosal are unique among archosaurs. Hence, some of these features must have either evolved independently in at least two separate lines among phytosaurs, or must have been secondarily lost in *Mystriosuchus*. It depends entirely on the most parsimonious placement of *Mystriosuchus* in the tree topology: this determines which character states represent true synapomorphies (homologues in the definition of PINNA 1991) indicating inheritance from a common hypothetical ancestor, and which are homoplasies or reversals that took place in the evolution of phytosaurs. It is the main aim of this section to identify the homoplastic characters.

Section 5.2

5.2.1 Phytosaur taxa included in the analysis

The following list includes the 22 taxa of Phytosauria which are incorporated in the analysis. With the exception of *Nicrosaurus* and *Mystriosuchus*, the systematics of which were treated in the chapters 2 and 3, this section is not intended as a systematic review of phytosaurs. Unless stated otherwise, the taxonomic scheme of the non-European phytosaurs largely follows LONG & MURRY (1995), but I will express my concerns about the validity of some taxa if necessary. I do not wish to draw taxonomic conclusions, however obvious from published data, before having studied the type material and referred specimens first hand. The genus *Paleorhinus* (*sensu* BALLEW 1989) or Paleorhininae of LONG & MURRY (1995), respectively, was broken up into its constituent species, and each taxon was scored separately to test the postulated monophyly of the group. For this reason, I have not eliminated a number of rather dubious species from the analysis, and consequently also retained some generic names which are generally regarded as junior synonyms of *Paleorhinus*.

The data for *Nicrosaurus* and *Mystriosuchus* have been presented in chapters 2 and 3. Character states in the remaining taxa were scored on the basis of published records only, and it is noted when studies other than the type description were consulted. I accept that this represents a source of potential errors, since it became only too obvious in the

course of the studies of *Nicrosaurus* and *Mystriosuchus* that descriptions of even well-preserved specimens of "well-known" taxa may contain significant misinterpretations.

Ebrachosuchus KUHN, 1936

OTU 1: *Ebrachosuchus neukami* KUHN, 1936 [type species]

Francosuchus KUHN, 1932

OTU 2: *Francosuchus broilii* KUHN, 1932 [type species]

Species included: *Francosuchus latus* KUHN, 1932; *Francosuchus angustifrons* KUHN, 1936.

Out of KUHN's four nominal species from one site in Franconia, recent workers have accepted only one as valid. The species name has been inconsistently identified in the past: either as *Paleorhinus neukami*, the remaining three being *nomina dubia* (HUNT & LUCAS 1991; LONG & MURRY 1995), or all four were synonymised with the senior binomen *Francosuchus broilii*, either as a distinct genus (CHATTERJEE 1978) or subgenus within *Paleorhinus* (GREGORY 1962a; WESTPHAL 1976). I coded *Francosuchus* (largely based on the best preserved specimen, the type of *Francosuchus angustifrons*, rather than the holotype of the type species) and *Ebrachosuchus neukami* separately to test whether the analysis supports a monophyletic clade of European primitive phytosaurs.

Mesorhinosuchus KUHN, 1961 [1961b]

OTU 3: *Mesorhinosuchus fraasi* (JAEKEL, 1910) [type species]

The taxon *Mesorhinosuchus* is shrouded in mystery. Not only was the single type skull rather poorly preserved and open to different interpretations, but it was allegedly derived from Early Triassic strata (middle Buntsandstein). No stratigraphical hypothesis or anatomical observation can be tested or checked any more, because the fragmentary skull was lost in World War II. The specimen is currently considered an indeterminable primitive phytosaur (CHATTERJEE 1978; BUFFETAUT 1993) or *Paleorhinus* sp. (HUNT & LUCAS 1991), but in the past even its phytosaurian nature was doubted (GREGORY 1962a, 1969; WESTPHAL 1976). *Mesorhinosuchus* is included in the analysis because the skull clearly shows the phytosaurian synapomorphies (1), (2), (5), (8), (9), and (12) listed in 5.3.1. Furthermore, the specimen was apparently even more primitive than any other phytosaur in having (6) the nasals not extended beyond the nares and (7) the septomaxillae positioned deeply at the base of the external nasal opening (HUENE 1911). However, both character states might have been erroneously reconstructed because of

poor preservation. The only available sources are the type description (JAEKEL 1910) and comments on the specimen by HUENE (1911). Some of the character codings may be questionable, because JAEKEL only presented a reconstruction of the type, which is hypothetical regarding snout length, details of the palatal configuration, and parts of the occipital aspect, and the type specimen was an incomplete, small skull (330 mm as preserved) and might have been a juvenile individual.

Paleorhinus WILLISTON, 1904

OTU 4: *Paleorhinus bransoni* WILLISTON, 1904 [type species]

Although a number of complete skulls are known (e.g. GREGORY 1962a; BALLEW 1989; LONG & MURRY 1995), the description of the type skull by LEES (1907), which is evidently misinterpreted in some features (MEHL 1915, 1928a; JAEKEL 1910; LANGSTON 1947), is actually still the only available source.

OTU 5: *Paleorhinus magnoculus* DUTUIT, 1977 [DUTUIT 1977b]

(= *Arganarhinus magnoculus* (DUTUIT, 1977) LONG et MURRY, 1995)

It has been argued above that many characters included in the specific diagnoses presented by DUTUIT (1977b) and HUNT & LUCAS (1991) are either individually variable among phytosaurs (jugal excluded from the orbit; exact position of the nares) or may represent juvenile characters (large size of the orbit; small antorbital and infratemporal fenestrae). The rejected character states include all characters used by LONG & MURRY (1995) to define the genus *Arganarhinus*, and consequently *Arganarhinus* is not accepted here. However, the type skull as figured and reconstructed in DUTUIT (1977b: pl. 1, figs. 1-2) shows the quadrate foramen visible in lateral view, in contrast to the posteriorly open foramen that is common to most of the other primitive phytosaurs. Additionally, DUTUIT found a number of unique characters in the type specimen: the palatine is extraordinarily long, the postorbital section of the skull is elongated, and the skull shows a unique configuration of the cheek including a non-subtriangular quadratojugal and a large lateral exposure of the quadrate. Pending a verification of the reconstruction, these features could well represent diagnostic characters of a distinct species, which is referred to here as *Paleorhinus magnoculus*.

OTU 6: *Paleorhinus sawini* LONG et MURRY, 1995

Almost all diagnostic characters of *Paleorhinus sawini* appear to be related to a tripartite strongly heterodont dentition (expanded posterior premaxilla and maxilla, enlarged maxillary alveoli, short rostrum, few teeth positions), although there is no direct evidence for the nature of the dentition preserved. Unfortunately, the type specimen and

only skull known has never been described, and many character states had to be scored provisionally using photographic evidence only (LONG & MURRY: fig. 24A-C). MURRY (1986) provided further data on tooth position numbers and the prenarial length, but numerous features are unavailable at present.

OTU 7: *Paleorhinus scurriensis* LANGSTON, 1949

HUNT & LUCAS (1991) and LONG & MURRY (1995) synonymised this taxon with *Paleorhinus bransoni*. It is retained in this analysis as a separate species because the type specimen has been described as showing a number of different character states compared to the type species of *Paleorhinus* (LANGSTON 1947).

"Parasuchus" LYDEKKER, 1885

OTU 8: "*Parasuchus hislopi*" LYDEKKER, 1885 [type species]

The type series of *Parasuchus hislopi*, including the snout fragment designated as lectotype by CHATTERJEE (1974), is generally accepted as undiagnostic (HUNT & LUCAS 1991; LONG & MURRY 1995). For this reason, the name is here restricted to the lectotype, and reference to other material is indicated by quotation marks. The characters were scored on the basis of the description of two skulls referred to *Parasuchus hislopi* by CHATTERJEE (1978).

Promystriosuchus CASE, 1922

OTU 9: *Promystriosuchus ehlersi* CASE, 1922 [type species]

The quality of the character scores relies largely on the accuracy of CASE's (1922) reconstruction, the only descriptive account of the taxon. *Promystriosuchus ehlersi* is not universally accepted: HUNT & LUCAS (1991) consider the type skull a specifically indeterminable specimen of *Paleorhinus* because of poor preservation, whereas LONG & MURRY (1995) tentatively retain its identity as a species of *Paleorhinus*, but in contrast to GREGORY (1962a) restrict the taxon to the holotype. This view is adopted here.

Angistorhinus MEHL, 1913

OTU 10: *Angistorhinus grandis* MEHL, 1913 [type species]

OTU 11: *Angistorhinus talainti* DUTUIT, 1977 [1977a]

Brachysuchus CASE, 1929

OTU 12: *Brachysuchus megalodon* CASE, 1929 [type species]

Having been united with *Smilosuchus gregorii* at times (GREGORY 1969), *Brachysuchus megalodon* is now generally accepted as a phytosaur species referable to *Angistorhinus* (LONG & MURRY 1995) or representing a distinct genus within closely related to *Angistorhinus* (HUNT 1994). All data for *Brachysuchus* were gathered from the well described and illustrated type skull (CASE 1929, 1930, 1932a).

Rutiodon EMMONS, 1856

OTU 13: *Rutiodon carolinensis* EMMONS, 1856 [type species]

Species included: *Rhytidodon rostratus* MARSH, 1896.

I follow the suggestions of DOYLE & SUES (1995) and LONG & MURRY (1995) to restrict the genus *Rutiodon* to the species *Rutiodon carolinensis*, which comprises the small, slender-snouted phytosaurs from the Newark Supergroup of eastern North America. References to more inclusive views of the genus "*Rutiodon*" (e.g. GREGORY 1962a, WESTPHAL 1976, BALLEW 1989) are indicated here by quotation marks. DOYLE & SUES (1995) demonstrated convincingly that *Rutiodon carolinensis* must be considered a metataxon *sensu* GAUTHIER (1986) at present. Character states were scored based on COLBERT (1947), GREGORY (1962a), and DOYLE & SUES (1995).

Leptosuchus CASE, 1922

OTU 14: *Leptosuchus crosbiensis* CASE, 1922 [type species]

Species included: *Leptosuchus studeri* CASE et WHITE, 1934; ? *Phytosaurus doughtyi* CASE, 1920 (*fide* LONG & MURRY 1995; this is in need of verification, since in the case of a subjective synonymy of *Phytosaurus doughtyi* with *Leptosuchus crosbiensis*, the species group name *doughtyi* would have priority).

Leptosuchus crosbienesis is scored on the basis of CASE (1922) and CASE & WHITE (1934).

OTU 15: *Leptosuchus adamanensis* (CAMP, 1930)

Species included: *Machaeroprosopus lithodendrorum* CAMP, 1930.

The data for *Leptosuchus adamanensis* is derived from the description of the type material by CAMP (1930).

Smilosuchus LONG et MURRY, 1995

OTU 16: *Smilosuchus gregorii* (CAMP, 1930) [type species]

According to the generic diagnosis in LONG & MURRY (1995), *Smilosuchus* differs from *Leptosuchus* mainly in characters which are related to the much more massive skull (gigantism, long prenarial crest, strong heterodonty, wider postorbital part of the skull, more dorsal orientation of the orbits and the infratemporal fenestrae). Similar differences are present in *Nicrosaurus kapffi* compared to the congeneric *Nicrosaurus* species B. It is questionable in my view whether such characters, which additionally are in parts subject to intraspecific variation in *Nicrosaurus kapffi*, justify the generic separation of *Smilosuchus*. The species is, nevertheless, the best known phytosaur taxon, being excellently described by CAMP (1930), with comments on a second specimen in COLBERT (1947).

Nicrosaurus O. FRAAS, 1866

OTU 17: *Nicrosaurus kapffi* (MEYER, 1860) [type species]

For a definition, synonymy, the specimen included in the taxon, and the morphological data, see subsection 2.2.2.

OTU 18: *Nicrosaurus* species B

For a definition, synonymy, the specimen included in the taxon, and the morphological data, see subsection 2.3.2.

Arribasuchus LONG et MURRY, 1995

OTU 19: *Arribasuchus buceros* (COPE, 1881) [type species]

Species included: *Machaeroprosopus andersoni* MEHL, 1922; *Machaeroprosopus tenuis* CAMP, 1930 [partim]; *Pseudopalatus mccauleyi* BALLEW, 1989; *Redondasaurus bermani* HUNT et LUCAS, 1993 [1993c].

The taxonomic concept of *Arribasuchus* in this study is adopted from LONG & MURRY (1995). The data is compiled from the studies, in which the type species and the referred taxa were erected, plus the figures of *Arribasuchus buceros* in HUENE (1915). However, since adequate descriptions of the types of "*Belodon*" *buceros* and *Redondasaurus bermani* are still wanting and *Machaeroprosopus andersoni* is represented by an incomplete and largely restored skull, it proved difficult to obtain reliable morphological information from the literature. For the same reason, it has yet to be convincingly demonstrated that the species included are indeed conspecific.

Pseudopalatus MEHL, 1928 [1928b]

OTU 20: *Pseudopalatus pristinus* MEHL, 1928 [1928b] [type species]

Species included: *Machaeroprosopus tenuis* CAMP, 1930 [partim, including the type specimen]; *Redondasaurus gregorii* HUNT et LUCAS, 1993 [1993c].

I follow LONG & MURRY (1995) in grouping together the type of *Pseudopalatus pristinus*, the uncrested specimens referred to *Machaeroprosopus tenuis* and the type species of *Redondasaurus* in a monotypic genus *Pseudopalatus* (contra BALLEW 1989). Alternatively, *Redondasaurus* would have been excluded because neither a full description nor accurate figures of the type specimen are available. Data were collected from MEHL's (1928b) description of the type specimen of *Pseudopalatus pristinus*, with additional evidence included from figured specimens in CAMP (1930), BALLEW (1989), and LONG & MURRY (1995).

Mystriosuchus E. FRAAS, 1896

OTU 21: *Mystriosuchus planirostris* (MEYER, 1863) [type species]

For a definition, synonymy, the specimen included in the taxon, and the morphological data, see subsection 3.2.2.

OTU 22: *Mystriosuchus* species B

For a definition, synonymy, the specimen included in the taxon, and the morphological data, see subsection 3.3.2.

5.2.2 Phytosaur taxa excluded from the analysis

Numerous phytosaur taxa are excluded from this phylogenetic study because only cranial characters are considered in the analysis. These include all genera represented by isolated teeth such as *Belodon* MEYER, 1844, *Centemodon* LEA, 1856, *Clepsysaurus* LEA, 1851, *Compsosaurus* LEIDY, 1856 [1856a], *Eurydorus* LEIDY, 1859, *Omosaurus* LEIDY, 1856 [1856b], *Palaeoctonus* COPE, 1877, *Paleosaurus* RILEY & STUTCHBURY, 1840, and *Suchoprion* COPE, 1877. Similarly, the binomina *Belodon lepturus* COPE, 1869 [in COPE 1869-71], *Belodon scolopax* COPE, 1881, *Belodon validus* LULL, 1915 *ex* MARSH 1893, *Clepsisaurus leaii* EMMONS, 1856, and *Rutiodon manhattanensis* HUENE, 1913 have been erected for isolated postcranial elements that cannot be scored. *Heterodontosaurus ganei* LUCAS, 1898, *Parasuchus hislopi* LYDEKKER, 1885, cf. *Francosuchus trauthi* HUENE, 1939, and aff. *Brachysuchus maleriensis* HUENE, 1940 are

based on snout or mandibular fragments and show such an amount of missing data that their position in the cladogram is highly unlikely to be resolved. All these taxa are of doubtful validity.

The following taxa are represented by more complete, and in most cases diagnostic, cranial material, but are not included in the analysis for the reasons given below:

Angistorhinopsis ruetimeyeri (HUENE, 1911). The binomen is based on a partial braincase with associated postcrania from the Knollenmergel Beds of Niederschönthal (Switzerland), which are most probably undiagnostic. Subsequently, a plethora of indeterminate, mostly isolated teeth and postcranial elements from various Rhaetic localities in central Europe have been attributed to *Angistorhinopsis ruetimeyeri*. In particular, HUENE (1922) referred a partial skull with articulated postcrania from Salzgitter to this species (Tab. 1.1). This specimen shares with *Pseudopalatus*, *Arribasuchus*, and *Mystriosuchus* a rounded parietal-supraoccipital complex with steep squamosal processes of the parietals (HUENE 1922: fig. 114a), suggesting a highly derived taxon. However, HUENE's (1922: figs. 128 - 130) reconstructions of the skull are composite and largely conjectural. I do not wish to include this specimen until the anatomy of the skull has been restudied, and the taxonomic status of *Angistorhinopsis ruetimeyeri* is resolved.

Four additional species have been named and were originally included in the genus *Angistorhinus*, and all are based on potentially diagnostic cranial material. The validity as well as the generic referral of these species are unclear at present (GREGORY 1962a; MURRY 1986; LONG & MURRY 1995). It is advisable first to re-examine the taxonomic status of the type specimens before analysing the phylogenetic relationships of these taxa.

Angistorhinus gracilis MEHL, 1915. MEHL (1915: 154) separated *Angistorhinus gracilis* from *Angistorhinus grandis* mainly on the basis of the more slender snout and characters that suggest a more gracile dentition. The type specimen, a skull with the mandible, was never illustrated, and was apparently not fully prepared when described.

Angistorhinus maximus MEHL, 1928 [1928a]. The taxon is based on the incomplete posterior part of a large skull. Compared to the type species, *Angistorhinus maximus* shows a long and narrow supratemporal fenestra, the postfrontal participates in forming its anterior border, and the posterior process of the squamosal is more elongate (LONG & MURRY 1995). Furthermore, the exoccipital seems to be well separated from the opisthotic and reaches the posttemporal fenestra. *Angistorhinus maximus* is considered by LONG & MURRY (1995) to represent a distinct genus yet to be named.

Angistorhinus alticephalus STOVALL et WHARTON, 1936. Based on the skull and nine dorsal vertebrae of one individual, *Angistorhinus alticephalus* is distinguished from other Angistorhininae by a very high postorbital skull and the nares being strongly elevated above level of the skull roof. There are a number of angistorhinine skulls available that show these features (GREGORY 1962a; LUCAS *et al.* 1993; MURRY 1989). However, the only available description by STOVALL & WHARTON (1936) is too superficial, and the reconstruction provided too schematic to allow a meaningful scoring of most of the characters used in the analysis.

Angistorhinus aeolamnis EATON, 1965. The type of *Angistorhinus aeolamnis* is a skull lacking the mandibles, and large portions of the narial region and the skull roof are unavailable because of erosion. It was placed in synonymy with *Angistorhinus* (= *Brachysuchus*) *megalodon* by LONG & MURRY (1995). According to the description, the specimen differs from other Angistorhininae in the maxilla being excluded from the choana and, unique among phytosaurs, the premaxilla reaching far posterior along the palatine to the suborbital opening.

Coburgosuchus goeckeli HELLER, 1954. HELLER named, described and illustrated a skull lacking the snout and the mandible from the upper Burgsandstein of Franconia (Tab. 1.1). The specimen has been frequently neglected in phylogenetic studies of phytosaurs, or was referred to the genus *Phytosaurus* (= *Nicrosaurus*) by HUENE (1956) and KUHN (1961a, b). However, the generic reidentification is based on the superficial similarity of the type skull to *Nicrosaurus kapffi* rather than on shared derived characters with the genus *Nicrosaurus* in my definition. *Coburgosuchus goeckeli* is not considered phylogenetically until I have the opportunity to study the specimen personally.

Leptosuchus imperfecta CASE, 1922. CASE introduced this species "tentatively, until a more detailed study can be made" (1922: 68) on the basis of a complete skull. He figured the type in 1924, but no description nor a differential diagnosis was ever provided. Hence, I agree with LONG & MURRY (1995) who considered *Leptosuchus imperfecta* a *nomen nudum*.

Machaeroprosopus validus MEHL, 1916. Previous reviewers of North American phytosaurs did either not consider (GREGORY 1962a, LONG & MURRY 1995) or dismissed the validity (BALLEW 1989) of *Machaeroprosopus validus*, the type species of *Machaeroprosopus* based on a skull lacking only the palate and parts of the cheeks, but with an associated mandible, on two grounds: firstly, the type specimen is lost, and,

secondly, MEHL's illustrations are regarded as reconstructions that cannot be vindicated any more (BALLEW 1989: 324; LONG & MURRY 1995: 229).

The taxonomic procedure followed in these reviews is inappropriate. According to Article 75(b) ICZN, a species group lacking the type specimen is neither invalid nor a taxonomic question resulting from its absence must be evaded, provided

> "a neotype is essential for solving a complex zoological problem, such as the confused or doubtful identities of closely similar nominal species group taxa for one or more of which no holotype, lectotype, or syntype is known to exist (ICZN, p. 175).

This requirement is definitely given by the unclear status of the genus *Machaeroprosopus* and the species groups that have been erected or later referred to this genus by MEHL (1916, 1922), CAMP (1930) and COLBERT (1947). Regarding the second argument, MEHL (1916) clearly distinguished *in litteris* between preserved original parts and restored or reconstructed parts of the type skull, and indicated this in the figures 1 to 5 provided in his description.

According to MEHL (1916), the type of *Machaeroprosopus validus* shows the following characters: a partial prenarial crest is present, the nares are positioned between the antorbital fenestrae and well above the level of the skull roof, the postorbito-squamosal bar covers most of the supratemporal fenestra, the posterior process of the squamosal is long (84 mm), the posttemporal fenestrae are large, and the parietal-supraoccipital complex appears to be rounded dorsally with steep lateral rims. The last feature is not fully comprehensive from the account and the figures given. These character states are in accord with the definition given for the genera *Arribasuchus* LONG et MURRY, 1995 (the authors indicate a synonymy on p. 3, but fail to draw the necessary nomenclatural conclusions in the systematic part), and *Pseudopalatus* both *sensu* BALLEW (1989) and HUNT (1993b). Other characteristics described for *Machaeroprosopus validus* such as short frontals, the supraoccipital not reaching the posttemporal fenestra, and the paroccipital process of the opisthotic not contacting the parieto-squamosal bar lateral to the posttemporal fenestra need to be compared with the type specimens of the various species that have been included in *Arribasuchus* and *Pseudopalatus* recently (*Belodon buceros*, *Machaeroprosopus andersoni*, *Pseudopalatus pristinus*, and *Pseudopalatus mccauleyi*). The situation is not fully intelligible from the available descriptions of these species.

I refrain at present from drawing definite conclusions regarding the synonymy of *Machaeroprosopus validus*. Further investigation is required, and taxonomic consequences must be the result of a comprehensive first-hand review of the taxa in question (ICZN, Art. 75(b)(i)), which is not the scope of this study.

5.2.3 Outgroups

The transformations of the character states used in the analysis are polarised by comparison with two close outgroups. The taxon chosen as primary reference is *Euparkeria capensis* BROOM, 1905, coded according to the redescription by EWER (1965). In the most recent phylogenies of archosaurs presented, *Euparkeria* was identified as the sistergroup to crown-group Archosauria (= Crurotarsi + Ornithodira) + Proterochampsidae (e. g. SERENO & ARCUCCI 1990; SERENO 1991; PARRISH 1993; JUUL 1994) or the direct sistergroup of crown-group Archosauria (BENTON & CLARK 1988). In the cases of inapplicable characters in *Euparkeria* (characters 3, 7-8, and 45), the plesiomorphic character state is supposed to be represented in primitive ingroups within Phytosauria ("non-phytosaurid phytosaurs"). In some characters, additional information is gathered to test the validity of supposedly plesiomorphic character states by comparison with the best known representatives of crurotarsan clades which are more derived than phytosaurs. These include aetosaurs (*Stagonolepis*: WALKER 1961), ornithosuchians (*Ornithosuchus*: WALKER 1964), and sphenosuchians (*Sphenosuchus*: WALKER 1990).

A second outgroup is represented by *Proterochampsa barrionuevoi* REIG, 1959 (SILL 1967), which is included because the taxon shares numerous cranial similarities with phytosaurs. Indeed, *Proterochampsa* has been interpreted as the oldest and most primitive phytosaur (WALKER 1968). However, based on postcranial characters, *Proterochampsa* as a highly derived member of the Proterochampsidae (including also *Cerritosaurus*, *Chanaresuchus*, and *Gualosuchus*: SUES 1976) is currently regarded as non crown-group archosaur (ROMER 1972; BENTON & CLARK 1988, SERENO & ARCUCCI 1990; SERENO 1991; PARRISH 1993, JUUL 1994) that acquired convergently a number of phytosaur skull characteristics. In addition to those listed for *Euparkeria* above, the characters 38 and 40 - 42 are not applicable for *Proterochampsa*, and are treated in a similar way.

Section 5.3
Character discussion

5.3.1 Characters constituting the monophyly of Phytosauria

Although Phytosauria has been regarded as a natural group for a long time and ROMER presented a composition of Phytosauria that matches the currently accepted opinion for the first time already in 1945, the group has been defined as a monophylum by shared derived characters only quite recently (BENTON & CLARK 1988; BALLEW 1989; SERENO 1991; PARRISH 1993; DOYLE & SUES 1995; LONG & MURRY 1995). I give a compilation of the cranial synapomorphies below, including three character states that have not been suggested so far. I add comments only on those characters which have a bearing on the features or character states used in the phylogenetic analysis.

In this study, the name Phytosauria JAEGER, 1826 is preferred. This is mainly for reasons of priority (see DOYLE & SUES 1995), but also because the alternative name Parasuchia LYDEKKER, 1888 in its original definition and its pre-ROMERian usage included, by contrast to Phytosauria, in almost all cases at least one representative of the Aetosauria.

5.3.1.1 Synapomorphies

(1) premaxillae posteriorly enlarged to a prenarial length equalling or exceeding the postnarial length of the rostrum. This results in the nares not being situated terminally.

(2) a suite of snout characters linked to "adaptations to piscivory" (SERENO 1991), including an increased number of teeth, a looser spacing of the teeth, an elongated and slender snout, essentially parallel snout margins, and an elongated mandibular symphysis.

(3) greatly increased size of the anteriormost two premaxillary and three dentary teeth, resulting in a lateral expansion of the jaw extremities.

(4) tip of the premaxillae distinctly downturned.

In contrast to SERENO's (1991) opinion, the apomorphic character states (3) and (4) are not necessarily a prerequisite of piscivorous predators, and are therefore listed separately. Greatly elongated, fang-like anteriormost teeth are relatively uncommon among fish-catching reptiles; such fangs are not developed, to quote only examples among predominantly piscivorous crocodiles as represented by the extinct teleosaurids, metriorhynchids, and the modern gharial *Gavialis* and the false gharial *Tomistoma*. The combination of long, slender, and low snouts with gently inflected, hooked premaxillae is unparalleled not only among crown-group Archosauria, but to my knowledge among tetrapods showing adaptations to a piscivorous semiaquatic or aquatic life style (e.g. trematosaurid temnospondyls, ichthyosaurs, choristoderes, and cetaceans).

(5) nares close to the midline of the skull, facing dorsally and showing rims that are raised to different degrees above the surrounding skull surface

(6) nasals extend anteriorly along the sides of the nares, terminating in front of these openings.

(7) paired paramedian "septomaxillae" (see comments on the nature of that bone in part 2.2.3.3).

(8) orbits directed more dorsally than in basal archosaurs (but paralleled in *Doswellia* and *Proterochampsa*), ornithodirans, and (non-crocodilian) crocodylomorphs.

Although there is much variation regarding this character among phytosaur taxa and within the OTUs of this study, and the character is therefore unsuitable for a resolution of ingroup clades, this generalised definition is correct.

(9) quadratojugal subtriangular.

(10) squamosal subdivided in a horizontal and a vertical plane.

This character was first introduced by BALLEW (1989), and has been subsequently adopted to characterise Phytosauria (SERENO 1991, LONG & MURRY 1995). However, it should be noted that also *Doswellia* shows the same separation of the squamosal (WEEMS 1980: fig. 8). The derived character state does not include *a priori* the presence of a lateral ridge on the squamosal as suggested by BALLEW (1989: 316), which enhances greatly

the morphological distinction between both squamosal planes. This structure is treated separately as an ingroup feature (character 27 of the analysis).

(11) skull dorsoventrally flattened, resulting in the occipital aspect being at least twice as wide as high.

The reduced skull height observed in all primitive phytosaurs is not unique among archosaurs as stated in SERENO (1991), but is paralleled in *Proterochampsa* (SILL 1967), *Doswellia* (WELLS 1980), and numerous Crocodilia. It should be noted that the character is intraspecifically variable to some degree (*Nicrosaurus*, subsection 2.2.7 and part 2.3.4.2) and apparently reversed independently in several more advanced taxa (e.g. *Mystriosuchus*, this study; *Leptosuchus crosbiensis*, cf. CASE & WHITE 1934).

(12) dorsally arched palatal vault and lateral shelves of the palatines with palatal ridges, supporting most probably a secondary soft palate.

(13) suborbital fenestra reduced to a broad slit (not to a foramen, *contra* SERENO 1991).

Although being considerably reduced in size compared to the outgroups, the suborbital fenestra of a number of phytosaurs may still be broad (e.g. *Paleorhinus scurriensis*; *Mesorhinosuchus*) compared to more derived phytosaurs. The narrow slit-like, or further reduced, suborbital fenestrae are regarded here as apomorphic ingroup states (for further discussions, see character 47).

The following character states are introduced as synapomorphic for Phytosauria here for the first time:

(14) presence of two well-defined alveolar ridges on the premaxillae and maxillae which enclose an interpremaxillary fossa.

(15) broad and flat dorsal aspect of the symphyseal region of the mandible (paralleled in crocodiles), which is considerably elevated above the level of the alveoli to a symphyseal platform.

(16) quadrate foramen at mid-height of the quadrate, and subround or round in shape.

In the archosaurs showing a persisting quadrate foramen, the opening is invariably located in the lower third of the quadrate. In the immediate outgroup of Phytosauria, *Euparkeria*, the quadrate foramen is large and forms a dorsoventrally elongated, slit-like

passage between quadrate and quadratojugal (EWER 1965). In Phytosauria, the quadrate foramen is clearly positioned further up the quadrate, and may reach a position below the lateral extremity of the paroccipital process of the opisthotic. The actual opening is enclosed in a much larger recess which broadly corresponds in size and outline to the foramen quadrati of *Euparkeria*. This suggests that the lumen of the foramen quadrati has already been reduced in the ancestral line of phytosaurs. More importantly, the shape of the foramen is always rounded, rather than slit-shaped (*Euparkeria*), or an irregular angular opening (e.g. *Chasmatosaurus*: CRUICKSHANK 1972; *Stagonolepis*: WALKER 1961). The size of the foramen is further reduced within phytosaurs (character 41).

5.3.1.2 Dubious or rejected synapomorphies

(i) premaxilla contacts the palatine on the surface of the palate (SERENO 1991).

The character seems to be variable among phytosaurs and was therefore included in the phylogenetic analysis (character 44). It is sufficient to say here that the premaxilla evidently does not touch the palatine externally in ventral view in *Nicrosaurus* and *Mystriosuchus* (chapters 2 and 3), rendering the validity dubious for the whole group.

(ii) presence of a paroccipital process of the squamosal.

The character was originally suggested by BALLEW (1989: character 10, node C) as synapomorphic for an unnamed ingroup that corresponds to the Phytosauridae as defined by DOYLE & SUES (1995). Actually, a downward projecting paroccipital process of the squamosal braced medially against the opisthotic is consistently present in all phytosaurs in which this region has been adequately described or figured. Moreover, a distinct process of the squamosal in touch with the lateral end of the paroccipital process of the opisthotic occurs also in at least some aetosaurs (WALKER 1961: figs. 2b, 4d), ornithosuchians (WALKER 1964: fig. 5a; SERENO 1991: figs. 11-12), rauisuchians (LONG & MURRY 1995: fig. 123c), and sphenosuchians (WALKER 1990: fig. 2a; SERENO & WILD 1992: fig. 10). However, different names have been used for this obviously homologous structure (e.g. posterior process, SERENO & WILD 1992), which are easily confused with similarly named, non-homologous structures in phytosaurs. It is, however, only in phytosaurs that the paroccipital process of the squamosal extends directly ventrally. In the majority of phytosaurs (but not all - see character 41 of this study) the process increases to a very prominent structure projecting ventrally far below the opisthotic. I do not propose that the ventral direction of the process is synapomorphic for phytosaurs; it might be difficult to recognise such character states precisely as long as the individuality of the process is not fully developed. Basal archosaurs (CRUICKSHANK

1972; EWER 1965) and ornithodirans (e.g. COLBERT 1989; GALTON 1984, 1985a) lack a clearly defined process, as do crocodiles. The character distribution might rather suggest that the development of a distinct process of the squamosal supporting the extremity of the opisthotic is a derived character state of Crurotarsi, later reversed within crocodylomorphs.

5.3.2 Characters included in the analysis

The following discussion lists the 49 characters that were utilised to reconstruct the phylogeny of phytosaurs. However, a number of characters (notably 19, 37, 43, and 44) are not entirely satisfactory and are included in the analysis, but identified as still problematic requiring further investigation. Some of the multistate characters are followed by an internested set of binary definitions that are employed to characterise clades in Figures 5.5 and 5.6, and in subsection 5.4.3. The derived character states 11, 46 and 49 characterise *Nicrosaurus*, and 1[3], 12, 14, 15[2], 24[2], and 42 have been identified as diagnostic for *Mystriosuchus*. These character states are more extensively described and discussed, if necessary, in subsection 2.1.2 and part 3.1.2.1.

(1) snout length, expressed by the ratio of the preorbital skull length to the orbital + postorbital skull length: short, < 1 (0) - moderate, 1 - 2.9 (1) - long, 3 - 3.49 (2) - very long, > 3.5 (3); see Appendix B, Table B.1

(1[1]) short, <1 (0) - moderate to very long, ≥1 (1)

(1[2]) short to moderate, <3 (0) - longer, ≥3 (1)

(1[3]) short to long, <3.5 (0) - very long, ≥3.5 (1)

The preorbital length (in relation to the remaining skull length to remove autocorrelation, GREGORY 1962a) is preferred here as an index for snout length rather than prenarial length (= rostral length) as used by CAMP (1930), COLBERT (1947), GREGORY (1962a), CHATTERJEE (1978) and MURRY (1986), because the latter partially depends on the variable position of the nares leaving the values for non-phytosaurid phytosaurs incompatible with those for Phytosauridae (see Tab. B.1 and part 3.2.3.1). The effect of growth on the prenarial to the postnarial skull length in relation to total skull length has been discussed in depth by COLBERT (1947) and was interpreted in evolutionary terms ("trend lines") and illustrated in a graph in GREGORY (1962a: fig. 4). GREGORY concluded that negative relative "growth" of the rostrum is associated with size

within the genera *Paleorhinus*, *Mystriosuchus* and "*Rutiodon*" (i.e. the larger a species the shorter the rostrum), in contrast to an isometric trend in the rostrum length of "*Phytosaurus*". He considered the mode of growth, the growth rates, and the "initial" prenarial length (of an ontogenetic series) useful as discriminators for genera. These postulated "allometric" relationships apply for snout length as well. Major points of criticism include that ontogenetic terms such as "growth", "growth curve", and "growth rate" are confused with evolutionary relative length increase or taxonomic differences in skull proportions. More importantly, the taxonomic patterns of differential length increase of the rostrum, and the computed "growth rates", are identified as such by the congruence with the distribution of other characters deemed taxonomically significant (prenarial crests, dermal armour), and collapse when GREGORY's taxonomic scheme is abandoned. For example, no constant rate of a genus-specific "growth trend" is obvious when the plots for the genus "*Phytosaurus*" are separated into the constituting species *Nicrosaurus kapffi*, *Smilosuchus gregorii*, and *Brachysuchus megalodon*.

Euparkeria represents the primitive state for crurotarsans with the snout equalling or shorter than the orbital and postorbital part of the skull together. The snout in phytosaurs is considerably elongated (always more than two times the reference length), and the character is further subdivided here into moderate, long, and very long snouts. State (1) includes the second outgroup *Proterochampsa* plus *Paleorhinus magnoculus*, *Paleorhinus sawini*, *Angistorhinus talainti*, *Brachysuchus megalodon*, and all taxa with tripartite dentitions (including the type of *Arribasuchus buceros*, the polymorphic state resulting from the probably synonymous *Machaeroprosopus andersoni*). Long snouted forms (3 to 3.5 times the reference length) are represented by *Paleorhinus bransoni*, "*Parasuchus hislopi*", *Angistorhinus grandis*, *Rutiodon carolinensis*, *Nicrosaurus* species B, *Pseudopalatus pristinus*, and *Mystriosuchus* species B. *Ebrachosuchus neukami* (note that the exact snout length is unknown in *Francosuchus*; KUHN 1936, HUNT & LUCAS 1991), *Paleorhinus ehlersi*, and *Mystriosuchus planirostris* form a distinct cluster with a snout length of about four times the length of the remaining skull.

(2) ventral rim of the maxilla: straight (0) - convex ventrally (1)

Character state (1) is not necessarily correlated with the possession of extremely large maxillary teeth or the number of dental sets in the dentition, as could be expected. Taxa with fairly derived maxillary dentitions such as *Angistorhinus grandis* may show straight ventral alveolar borders. The convex ventral outline of the maxilla is common among tripartite heterodont forms, but is not expressed in both *Leptosuchus* species.

(3) internasal septum: premaxillae form the entire, or contribute substantially to the septum (0) - septum formed by septomaxillae alone (1)

In the outgroups, the premaxillae and the nasals alone form the internasal septum (state 0). In *Paleorhinus scurriensis*, paired septomaxillae are present, but in dorsal view the premaxillae separate these bones and contribute to the septum (LANGSTON 1947). In the other phytosaurs of which descriptions or figures of the narial region have been published, the septomaxillae are united in front of the nares and the premaxillae no longer participate in forming the internasal septum externally (state 1).

(4) lateral rim of the maxilla: straight or convex (0) - distinctly concave (1)

In the outgroup *Euparkeria* and almost all archosaurs, the lateral rim of the maxilla is either straight or convex, and this was taken as the primitive state (0). In the derived state (1), the lateral rim of the maxilla and the cheek is distinctly concave. This is the case in the second outgroup *Proterochampsa*, in *Ebrachosuchus neukami*, *Paleorhinus magnoculus*, *Pseudopalatus pristinus*, and both *Mystriosuchus* species. This character is essentially a more precise formulation of BALLEW's (1989) character 43, reading "skull triangular in outline", which in its literal meaning covers almost all phytosaur taxa, with perhaps the exception of especially broad-snouted forms such as *Brachysuchus*, *Smilosuchus*, and the robust morph of *Nicrosaurus kapffi*. BALLEW (1989) originally suggested a "triangular skull" as synapomorphic for the clade *Pseudopalatus* (here *Pseudopalatus* and *Arribasuchus*) + *Mystriosuchus*. However, the maxilla is not convex but straight in *Arribasuchus buceros*.

(5) nature of the dentition: laterally compressed, serrated teeth (0) - bipartite heterodont (1) - tripartite heterodont (2)

The dentition of Archosauria (= Archosauriformes of other authors) is characterised by the presence of laterally compressed teeth (BENTON & CLARK 1988), which are usually finely serrated. This is the case in the outgroup *Euparkeria*, the morphology of the dentition of *Proterochampsa* being unknown. As described in subsection 2.2.5, phytosaur dentitions are highly specialised in having (1) a set of greatly enlarged fangs followed by a diastema and (2) a post-fang dentition that consists of either one post-fang set (bipartite dentition) or is subdivided into two distinct arrays of teeth (premaxilla and maxilla sets) which both show a morphological gradation from unspecialised to highly differentiated tooth shapes (tripartite dentition). In all phytosaurs bilateral symmetrically compressed teeth are absent and specialised teeth show a flattened lingual face opposed by a vaulted labial side.

Because of the highly specialised dentitions, it is not immediately obvious which of the two different types outlined above is the plesiomorphic condition within Phytosauria. GREGORY (1962a) assumed the least specialised type in terms of complexity ("homodont", here included in bipartite heterodont) to be primitive. Furthermore, tripartite dentitions are unique to phytosaurs among archosaurs, and therefore most likely the more derived state. This polarity is supported by the observation, that there is no evidence for tripartite dentitions in more primitive and stratigraphically older phytosaurs (non-phytosaurid phytosaurs, Angistorhininae). The phytosaur taxa included in the analysis are scored according to Table 2.2.8. No attempt has been made to differentiate between degrees of heterodonty within bipartite and tripartite dentitions.

(6) number of teeth: low, ≤ 17 (0) - moderate, 18 - 47 (1) - high, ≥ 48 (2); see Appendix B, Table B.2

(6[1]) low, ≤ 17 (0) - moderate to high, ≥ 17 (1)

(6[2]) low to moderate, <48 (0) - high, ≥ 48 (1)

GREGORY (1962a) reviewed the significance of tooth counts for phytosaur taxonomy, and concluded that the number of teeth has a limited potential at generic level. However, his conclusions are in parts invalid by his more comprehensive and now universally abandoned composition of genera and species (e.g. his *Mystriosuchus* includes also *Nicrosaurus* species B, and his "*Rutiodon*" is subdivided here into *Rutiodon*, *Leptosuchus*, *Smilosuchus*, *Arribasuchus*, and *Pseudopalatus*). To facilitate comparison, I regrouped the majority of his data at species level in Appendix B (Tab. B.2).

The data set is not fully conclusive, probably because of two reasons. Firstly, it can be demonstrated in *Nicrosaurus kapffi* that the number of teeth is subject to substantial individual variation (see Tab. 2.2.3), and this might hold true for other taxa known only from a few specimens. Secondly, it is obvious that the character is negatively correlated with snout length (and probably also to some extent with the degree of heterodonty) for spatial reasons. However, the character has been included because this relationship is not linear: *Mystriosuchus* shows the same proportional snout length as *Ebrachosuchus* (the ratio of preorbital to orbital + postorbital skull length is 3.8 and 4, respectively; Tab. B.1), but *Mystriosuchus* is far outnumbered by *Ebrachosuchus* in the number of tooth positions.

In the outgroups, the number of teeth is considerably lower than in any phytosaur (a maximum of 17 teeth is present in *Proterochampsa*), which suggests that a low tooth number is a plesiomorphic state (0). A threshold within Phytosauria was arbitrarily set at

47 tooth positions, a number which is not exceeded by taxa with tripartite dentitions. The most derived character state (2) distinguishes *Ebrachosuchus* from all other primitive phytosaurs. Note that *Francosuchus*, which is usually synonymised with *Ebrachosuchus* from the same locality (CHATTERJEE 1978; HUNT & LUCAS 1991), shows a significantly lesser number of teeth (KUHN 1936). Furthermore, character state (2) supports the clade *Pseudopalatus pristinus* + *Mystriosuchus* .

(7) anterior extent of the septomaxilla relative to the tip of the nasal: posterior to or at level (0) - extends beyond nasal (1)

I agree with SERENO 1991 that the absence of a septomaxilla in all well known crown-group Archosauria except in Phytosauria and in the majority of basal archosaurs suggests a synapomorphic acquisition of the bone in phytosaurs (*contra* BENTON & CLARK 1988). Consequently it is reasonable to assume, that an expansion of the bone in an anterior direction is an apomorphic trait. The tip of the nasal is chosen as reference point for the anterior extend of the septomaxilla because in *Nicrosaurus kapffi* the relationship of these bones are found to be constant in contrast to the individually variable absolute length of the septomaxilla (part 2.2.7.1 (12)).

Angistorhininae retain consistently the primitive condition, whereas the character distribution is random among non-phytosaurid phytosaurs and more derived Phytosauridae, even within well-defined genera (e.g. *Nicrosaurus*). This suggests that in contrast to character (8), a secondarily elongation of the septomaxilla took place several times independently.

(8) septomaxilla extends behind the naris: absent (0) - present (1)

The polarity of this character is difficult to determine. The extent of the septomaxilla behind the naris is observed among all non-phytosaurid phytosaurs, in which the bone has been identified. The restriction of this state to the most primitive phytosaurs might suggest that a posterior expansion is the plesiomorphic condition in Phytosauria, with a subsequent reduction in the clade Phytosauridae. However, the character is polarised here the opposite way, according to the nares bound posteriorly by the nasal in the outgroups and the argument put forward for character (7).

(9) naris elevated beyond the level of the skull roof: absent (0) - present (1)

The problems involved with the elevation of the external nasal openings and the distribution of the character states among phytosaurs are discussed in part 2.3.4.1. Although there are doubts about the utility of the character, it is included in the analysis

pending further investigation. The derived character state occurs among the OTU's of the analysis only among specimens referable to *Arribasuchus buceros* and *Pseudopalatus pristinus*.

(10) position of the posterior rim of the naris: terminal or subterminal (0) - non-terminal, in front of the anterior rim of the antorbital fenestra (1) - non-terminal, at level with the anterior rim of the antorbital fenestra (2) - non-terminal, behind the anterior rim of the antorbital fenestra (3)

(10[1]) terminal or subterminal (0) - not terminal (1)

(10[2]) in front of antorbital fenestra (0) - at level or behind antorbital fenestra (1)

(10[3]) in front to at level of antorbital fenestra (0) - behind antorbital fenestra (1)

The terminal or subterminal position of the nares is the ancestral state (part 5.3.1.1, (1)). Non-phytosaurid phytosaurs show the nares shifted back to a position between the tip of the snout and the antorbital fenestrae (state 1), but in two species, *Mesorhinosuchus fraasi* and *Promystriosuchus ehlersi*, the nares are positioned further back, terminating at level with the reference openings (state 2). The posterior rim of the nares situated between the antorbital fenestrae (state 3) characterises Phytosauridae. Within character state (3), the exact position of the nares with regards to the antorbital fenestrae is individually, and probably also taxonomically, variable, as discussed in part 2.2.7.3.

Character 10 includes essentially another feature, the exact position of the internal relative to the external nasal opening, i. e. whether the anterior rim of the choanae is placed somewhat anterior to, below, or slightly posterior to the anterior rim of the nares. The position was considered to be phylogenetically important by CASE (1922, 1929), CAMP (1930), GREGORY (1962a), and recently by LONG & MURRY (1995). In non-phytosaurid phytosaurs, the choanae are situated posterior to the nares for at least one naris length, whereas in all other phytosaurs, the choanae are placed more or less directly beneath the naris. However, a comparison of all phytosaur genera shows that the position of the choana relative to a chosen fixed point of the skull (e.g. the centre of the orbit, MEHL 1916) is the same throughout. The relationship of the orbit to the naris in all phytosaurs is in accord with the condition in the outgroups, and probably represents the inherited plesiomorphic position of the choana. The location of the choanae relative to the external nasal opening thus represents an inevitable consequence of the elongation of the premaxillae, combined with the backward-shift of the nares in Phytosauridae. For this reason, the character is united here with the location of the nares relative to the orbits.

The location of the choana seems to be variable at species level (see part 2.2.7.2). It has also been suggested that posteriorly placed choana in Phytosauridae, in a position

similar to non-phytosaurid phytosaurs, is a juvenile character (CAMP 1930). This was substantiated by HUNT *et al.* (1997), provided their referral of the juvenile skull described in this paper to Phytosauridae is correct. Note that there is probably no functional difference between both character states since the morphology of the palate (presence of a palatal ridge) in all phytosaurs suggests strongly that the air passage was entirely separated from the oral cavity by a secondary soft palate.

(11) infranasal recess: absent (0) - present (1)

See discussion in subsection 2.1.2.

(12) preorbital depression: absent (0) - present (1)

See discussion in part 3.1.2.1.

(13) length of the prefrontal in comparison to the postfrontal: elongated, length ≥ 1.5 times the length of the postfrontal (0) - prefrontal shorter than 1.5 to subequal in length (1)

The prefrontal of *Euparkeria* is typical for basal archosaurs in being a slender bone that exceeds 1.5 times the length of the postfrontal (state 0). The phytosaurs *Mesorhinosuchus*, *Paleorhinus bransoni*, *Angistorhinus talainti*, and especially *Paleorhinus magnoculus* show the same length relationship, although the area of exposure on the skull (i.e. the width of the prefrontal) is significantly larger in comparison to *Euparkeria*. In all other taxa, the prefrontal and postfrontal are subequal in both length and size. The prefrontal of "*Parasuchus hislopi*" and *Pseudopalatus pristinus* is somewhat longer, but does not exceed 1.5 times the length the postfrontal (state 1).

(14) deep sculpture of the skull roof and the narial region: absent (0) - present (1)

See discussion in part 3.1.2.1.

(15) pre-infratemporal shelf: absent (0) - high and narrow (1) - broad (2)

(15[1]) absent or small recess (0) - narrow strip paralleling the anteroventral rim of the infratemporal fenestra (1)

(15[2]) absent or small recess (0) - broad and extensive shelf in the lower half of the infratemporal fenestra (1)

See discussion in part 3.1.2.1.

(16) anterior corner of the infratemporal fenestra: behind the orbit (0) - at level of the posterior rim to beneath the posterior half of the orbit (1) - beneath the anterior half of the orbit (2)

(16[1]) behind the orbit (0) - extends beneath the orbit (1)

(16[2]) behind to beneath the posterior half of the orbit (0) - beneath the anterior half of the orbit (1)

This character, first listed in CHATTERJEE (1978), is redefined and included as a readily determinable indicator of the size of the infratemporal fenestra relative to the skull within phytosaurs. Moreover, it probably gives also a rough estimation of the relative length of the postorbital region of the skull, independent from the presence and the length of a posterior process of the squamosal. *Paleorhinus magnoculus* is the only taxon showing the same primitive condition of the fenestra far behind the orbit as the outgroups (state 0). An infratemporal fenestra, enlarged in absolute terms (state 1), is common among non-phytosaurid phytosaurs, and occurs also in *Rutiodon carolinensis*. In almost all Phytosauridae, but also *Ebrachosuchus*, the distance between orbit and quadrate is abbreviated, causing the anterior section of the infratemporal fenestra to shift beneath the orbit (state 2).

(17) extent of the jugal bordering the antorbital fenestra ventrally: less than 50% (0) - 50% or more (1)

Euparkeria and the majority of phytosaurs show the jugal bordering less than the posterior ventral half of the antorbital fenestra (state 0). In *Angistorhinus grandis* and *Angistorhinus talainti*, the anterior process of the jugal contacting the maxilla is elongated and forms more than half of the ventral border of the opening (state 1). The situation is paralleled in the outgroup *Proterochampsa*.

(18) height of the jugal: ratio of minimum height of the quadratojugal process of the jugal to skull height at the same spot: low, ≤ 0.2 (0) - moderate, 0.21-0.29 (1) - high, ≥ 0.3 (2); see Appendix B, Table B.3

(18[1]) low, ≤ 0.2 (0) - moderate to high, > 0.2 (1)

(18[2]) low to moderate, < 0.3 (0) - high, > 0.3 (1)

The character "jugal is a much thinner [probably in the meaning of higher] bone before it meets the quadratojugal" was introduced by BALLEW (1989: character 35) to characterise the clade comprising *Nicrosaurus*, *Arribasuchus*, *Pseudopalatus* and

Mystriosuchus. The originally unprecisely defined character is here quantified in relation to skull height (Tab. B.3).

The polarity of the character is defined by the low, slender jugal of *Euparkeria*. *Nicrosaurus* species B, *Pseudopalatus pristinus*, and especially both species of *Mystriosuchus* show similarly slender jugals. The intermediate state (1) is the most common condition. High jugals according to the definition above (state 2) are found in *Paleorhinus magnoculus*, *Paleorhinus bransoni*, *Promystriosuchus ehlersi*, and *Smilosuchus gregorii*.

Although the primitive species grouped by BALLEW as *Paleorhinus* show generally a high jugal-quadratojugal bar (with the exception of "*Parasuchus hislopi*", in the upper range of state 1, and state 2), and the lowest figures are found in the most derived phytosaur taxa, it is impossible to distinguish *Angistorhinus* and *Brachysuchus* from the more derived Phytosauridae based on this character. Moreover, at least in the more derived phytosaurs the primitive character states 0 and 1 are obviously correlated with both the robustness of the skull and low skull height. For instance, robust taxa such as *Smilosuchus* and *Arribasuchus* differ widely in having higher jugal-quadratojugal bars compared to the more gracile *Leptosuchus* and *Pseudopalatus*, as do the robust and gracile morphs within *Nicrosaurus kapffi* ranging from 0.28 (SMNS 4379) to 0.19 (BMNH 42743). The character is thus unsuitable to define higher categories.

(19) jugal-quadratojugal suture: simple (?), the jugal terminates well in front of the quadrate ventrally (0) - squamal joint, the jugal reaches almost to the quadrate (1)

In all phytosaurs in which the cheek region has been described in adequate detail, the quadratojugal was found to be split ventrally into two vertical lamellae. These form a slot to receive a laterally compressed dorsal component of the jugal in a sandwich-like fashion. The squamal mode of articulation allows the jugal to expand along the ventral edge of the cheek while the enclosed lamina gradually decreases in height and the jugal finally underlies the quadratojugal along the ventral edge of the cheek as a thin process. Thus, the jugal in phytosaurs reaches far more posteriorly than in any other archosaur, and the quadratojugal generally contributes little to the ventral edge of the skull. In some specimens, the jugal terminates just next to the lateral mandibular condyle of the quadrate restricting the ventral surface of the quadratojugal entirely to a tiny area in the corner of the cheek. This condition (state 1) has been described so far for the genera *Brachysuchus* (CASE 1929), *Rutiodon* (COLBERT 1947), *Leptosuchus* (CASE 1920, 1922), *Smilosuchus* (CAMP 1930; CASE & WHITE 1934), *Nicrosaurus* (this study), and *Mystriosuchus* (MCGREGOR 1906; HUENE 1911; pers. obs.).

The exact nature of the quadratojugal-jugal suture has never been described for any non-phytosaurid phytosaur. However, some preliminary conclusions on the nature of the joint might be drawn from the length of the jugal in ventral view. *Paleorhinus bransoni* and to some extent *Promystriosuchus ehlersi* have been reconstructed with the same jugal-quadratojugal configuration as the taxa cited above (CASE 1922; LEES 1907), suggesting a similar mode of articulation. In *Francosuchus angustifrons* and *Ebrachosuchus neukami* (KUHN 1936), the posterior extent of the jugal is extensive as well. It must be noted, however, that Kuhn indicates a vertical, comparatively short, and thus perhaps simple joint between quadratojugal and jugal. This is contrasted by the reconstruction presented for "*Parasuchus hislopi*" (CHATTERJEE 1978), in which the jugal does not reach far backward along the lower edge of the cheek to the quadrate, but terminates considerably more anteriorly beneath the last quarter of the infratemporal fenestra. This is well in accord with the majority of crurotarsans (cf. SERENO 1991) and thus represents the plesiomorphic state (0) concerning the relative length of the jugal. It is implied here that the extent of the jugal in ventral view is an indicator for a still simple rather than a complex lamellar articulation between quadratojugal and jugal in these two taxa. Further investigation of the more primitive phytosaur taxa might reveal that the complex joint is a derived feature of all phytosaurs.

(20) length to width ratio of the postorbito-squamosal bar: slender, > 8 (0) - moderate, 8 - 4 (1) - broad, < 4 (2); see Appendix B, Table B.4.

(20[1]) slender, > 8 (0) - moderate to broad, ≤ 8 (1)

(20[2]) slender to moderate, ≥ 4 (0) - moderate to broad, < 4 (1)

The length of the postorbito-squamosal bar is defined here as the distance between the orbit and the insertion of the squamosal process of the parietal. The width represents the maximum transversal extension of the bar at the supratemporal fenestra. With the exception of *Nicrosaurus* and *Mystriosuchus*, the measurements are taken from published illustrations (Tab. B.4). The redefinition of the postorbito-squamosal bar length removes the effect of the variable length of the posterior process (see character 30), which probably explains the differing ratios of some taxa to those presented by MURRY & LONG (1989) and LONG & MURRY (1995).

In *Euparkeria* and more derived Crurotarsi (except Crocodylomorpha: WALKER 1990; SERENO & WILD 1992), the postorbito-squamosal bar is consistently a narrow strut, frequently with a rounded dorsal margin. The slender condition, the ratio being arbitrarily defined as more than 8 (state 0), corresponds largely to the nature of the

postorbito-squamosal bar in *Ebrachosuchus neukami*, *Brachysuchus megalodon*, and *Angistorhinus grandis*.

The majority of phytosaur taxa fall into an intermediate length-to-width class between 8 and 4 (state 1). Within this grouping, *Paleorhinus sawini*, *Paleorhinus scurriensis*, *Paleorhinus bransoni*, and especially *Promystriosuchus ehlersi* show rather high ratios, as does *Leptosuchus crosbiensis* in accord with the suggestion of LONG & MURRY (1995). *Paleorhinus magnoculus*, "*Parasuchus hislopi*", *Angistorhinus talainti*, and, by contrast to LONG & MURRY (1995), also *Leptosuchus adamanensis* and *Smilosuchus gregorii* have comparatively broader bars. According to the reconstruction by COLBERT (1947: fig. 8), *Rutiodon carolinensis* seems to be at the threshold to state (0), but the incomplete specimen described by DOYLE & SUES (1995) suggests a moderately broad postorbito-squamosal bar. This taxon is thus also scored as (1).

In *Nicrosaurus*, *Arribasuchus*, and *Pseudopalatus* (= Pseudopalatinae sensu LONG & MURRY 1995), the postorbito-squamosal bar is broad showing a ratio below 4 (state 2). The low values are in part correlated with the presence of a strong medial lamella of the squamosal (character 28), and thus with the closure of the supratemporal fenestra (CAMP 1930; COLBERT 1947), however, three taxa without or with very short lamellae and non-restricted fenestrae show a similar broadened postorbito-squamosal bar (*Francosuchus angustifrons* and both species of *Mystriosuchus*). *Proterochampsa* also falls well within broad postorbito-squamosal bars.

(21) length of the cojoined parts of the parietals relative to the length of the frontals: 50% or less (0) - more than 50% (1)

In *Brachysuchus* and *Angistorhinus*, the parietals appear to be elongated anteriorly, and the anterior (cojoined) parts of the bones are thus more than half as long as the frontals. The same character state is convergently achieved by *Proterochampsa*.

(22) posterior extent of the cojoined parietals relative to the supratemporal fenestrae: along half or more of the length of the fenestrae (0) - along less than half of the length of the fenestrae (1)

This character is adopted from BALLEW (1989: character 13), who identified this character as autapomorphic for *Angistorhinus*. However, the polarity has been reversed in this study, because in *Proterochampsa* (and most archosaurs), the parietals extend beyond the supratemporal fenestra. *Euparkeria* shows that the combined parietals and postparietals terminate on the skull roof at level of the midpoint of the supratemporal fenestrae, and this condition was chosen as a threshold. Character (22) is thus a measurement of the posterior median indentation of the skull roof. The reference point is

the supratemporal fenestrae rather than the tip of the squamosal to eliminate the bias that would result from the variable length of the posterior process of the squamosal.

In contrast to the distribution suggested in BALLEW (1989), the parietals remain united for more than half of the supratemporal fenestra (state 0) not only in *Angistorhinus* and *Brachysuchus*, but also in *Ebrachosuchus*, *Mesorhinosuchus*, and "*Parasuchus hislopi*" among more primitive phytosaurs. All other phytosaur taxa included in the analysis show the derived character state (1). Moreover, among these taxa the length of the supratemporal fenestrae covered by the cojoined parietals is at variance, ranging from almost 50% (*Mystriosuchus*) to 20% or less (*Arribasuchus buceros*: MEHL 1922; HUENE 1915). This probably reflects the degree of the indentation of the supratemporal fenestra into the skull roof, a character that was introduced by CAMP (1930) to distinguish between his species of *Machaeroprosopus*. Character state (1) is not further subdivided here because it proved difficult to establish satisfactory measurements from the specimens as illustrated, but the different degree of the indentation of the fenestra may indeed be an important taxonomic feature worthwhile further investigation.

(23) shape of both squamosal processes of the parietals: angular (0) - round (1)

This character is adopted from BALLEW's (1989) character 19. DOYLE & SUES (1995) correctly pointed out that squamosal processes of the parietals set at an angle to each other is not a synapomorphy of "*Rutiodon*" (*sensu* BALLEW 1989), as it is also shared by at least "*Parasuchus hislopi*" (CHATTERJEE 1978). The shape formed by the squamosal processes of both parietals is decoupled here from the direction of the processes in a vertical plane to compensate for DOYLE & SUES's criticism of BALLEW's (1989) definition of an angular and a rounded parietal-supraoccipital complex.

The outgroups, non-phytosaurid phytosaurs and Angistorhininae share the primitively angular squamosal processes that are at level with the skull roof. In further derived phytosaurs, the depression of the parieto-squamosal bar causes the squamosal processes to deviate from the horizontal plane and to slope downward (character 33). *Leptosuchus*, *Smilosuchus*, *Rutiodon*, and *Nicrosaurus* retain the angular morphology. I do not accept a further subdivision of state (0) according to the degree of slope and the angle enclosed between both processes (BALLEW 1989: character 39), because it is difficult to recognise discrete character states and both features are frequently affected by deformation (see part 2.2.4.3). The parietal processes become rounded at the top of the parietal-supraoccipital complex in *Arribasuchus*, *Pseudopalatus*, and both species of *Mystriosuchus* .

(24) overhang of the parietals over the supraoccipital shelf: absent (0) - overhang developed (1) - overhang forms a distinct horizontal ledge (2)

(24[1]) absent (0) - present (1)

(24[2]) absent or triangular overhang present (0) - horizontal ledge (1)

In *Euparkeria*, the skull roof terminates without hanging over the supraoccipital shelf (state 0). The condition in *Ebrachosuchus* and *Francosuchus* (KUHN 1936: pl. 10 figs. 3, 4) is regarded as broadly similar. BALLEW (1989: character 42) cited overhang of the parietals above the supraoccipital as a synapomorphy characterising *Arribasuchus*, *Pseudopalatus* and *Mystriosuchus*. However, an overhang of the parietals is actually figured in the occipital views of the second outgroup *Proterochampsa*, and the non-phytosaurid phytosaurs *Mesorhinosuchus*, *Paleorhinus bransoni* (suggestive from LEES 1907: fig. 1), *Paleorhinus scurriensis*, and *Promystriosuchus*. The overhang is better developed in *Nicrosaurus* in the form of a groove along the squamosal processes (see subsection 2.3.3; Fig. 2.54), and a triangular roof at the apex of the parietal-supraoccipital complex (Fig. 2.11). *Rutiodon carolinensis* shows a comparable condition (GREGORY 1962b: figs. 3, 4), as do *Leptosuchus* and *Smilosuchus*. BALLEW's character 42 is rephrased here in a more precise definition: the presence of an overhang in general is coded as (1). As a more derived state (2), such an overhang is developed as a distinct transverse ledge in *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus* (further discussed in part 3.1.2.2, (iv)). A comparable horizontal ledge, however, is not restricted to the these taxa, but has also been figured in the angistorhinine phytosaurs included in the analysis (CASE & WHITE 1934: pl. 8 fig. 2; DUTUIT 1977a: fig. 2B, fig. 3; MEHL 1915: fig. 5). The presence of a parietal ledge is thus a separate character, decoupled from the transversely narrow, rounded parietal-supraoccipital complex.

(25) anterior border of the supratemporal fenestra: level with the surrounding skull roof surface (0) - raised (1)

See discussion in part 3.1.2.1.

(26) groove on the dorsal surface of the squamosal: absent (0) - present (1)

The planar dorsal surface of the squamosal in all non-phytosaurid phytosaurs is characterised by the presence of a shallow, elongated depression (state 1). Such a groove is absent in other phytosaurs and both outgroups (state 0), with the exception of *Rutiodon carolinensis*, which is polymorph regarding this character (DOYLE & SUES 1995).

(27) prominent and sharp ridge separating the dorsal from the lateral plane of the squamosal, overhanging the latter: absent (0) -present (1)

A derived condition in phytosaurs is the separation of the squamosal into two planar components in a horizontal and vertical plane, respectively (see subsection 5.4.1). In the non-phytosaurid phytosaurs, the lateral edge between both planes above and behind the infratemporal fenestra is marked by a prominent longitudinal ridge that overhangs the cheek (GREGORY 1962a: 671; BALLEW 1989: 333). The same character is also clearly distinguished in both species of *Mystriosuchus*. A squamosal ridge is absent in *Brachysuchus*, *Leptosuchus*, *Smilosuchus*, and most *Nicrosaurus* specimens, in which the horizontal surface of the squamosal is either convex or strongly reduced (character 28), and the distinction between the horizontal and vertical plane of the squamosal is generally less pronounced. A distinct ridge in similar position has also been reported for *Angistorhinus talainti* (DUTUIT 1977a: 322) and *Rutiodon carolinensis* (DOYLE & SUES 1995). It is also present in two specimens of *Nicrosaurus*, SMNS 5727 *Nicrosaurus kapffi* and BMNH 42745 *Nicrosaurus* species B, and figured specimens of *Pseudopalatus pristinus* suggest the presence of a squamosal ridge as well (e.g. BALLEW 1989: pl. 6 fig. C, pl. 7 fig. C). However, in *Nicrosaurus* at least the ridge is never as sharp and conspicuous as in, for instance, *Mystriosuchus*. This distribution suggests indeed that a ridge-like structure along the dorsal rim of the squamosal (and probably a lateral groove observed on the vertical part of the bone in some taxa: LONG & MURRY 1995) is a consequence of the development of distinctively separated surfaces of the squamosal, being synapomorphic of Phytosauria. The development of the ridge in non-phytosaurid phytosaurs and *Mystriosuchus* (described in detail in part 3.3.2.1; Fig. 3.5) is readily recognisable and clearly different from the other taxa. Thus, the character state of BALLEW and LONG & MURRY has been rephrased, to express the meaning intended by these authors, and is incorporated in the data matrix.

(28) development of a medial lamella of the parieto-squamosal bar: absent (0) - present, but narrow (1) - moderate, closes at least half of the width of the supratemporal fenestra in dorsal view (2) - strong, may close the entire supratemporal fenestra (3)

(28[1]) absent (0) - present (1)

(28[2]) absent, or narrow (0) - moderate to strong (1)

(28[3]) absent, or narrow to moderate (0) - strong (1)

It is assumed on the basis of the available descriptions and illustrations that non-phytosaurid phytosaurs, *Angistorhinus grandis*, *Brachysuchus megalodon*, *Leptosuchus*

crosbiensis, and *Smilosuchus gregorii* do not possess a medial lamella of the squamosal (state 0). However, this is not explicitly stated in the literature, and needs to be checked in the specimens. Character state (1) is described and illustrated for *Mystriosuchus* (part 3.3.2.1; Fig. 3.6), and is similarly coded for *Rutiodon* on the basis of the fairly large supratemporal fenestra, and a broader postorbito-squamosal bar than *Smilosuchus gregorii* and *Leptosuchus crosbiensis* in dorsal view (DOYLE & SUES 1995). In contrast to LONG & MURRY (1995), I interpret *Leptosuchus adamanensis* as having a narrow medial lamella as well, at least in the posterior part of the supratemporal fenestra (CAMP 1930: pl. 2). *Nicrosaurus* exhibits character state (2), in which the supratemporal fenestra is partly covered by the medial lamella of the squamosal (part 2.2.3.3). The reduced width of the supratemporal fenestra suggests this also applies for *Angistorhinus talainti* (DUTUIT 1977a). State (2) is further discussed, along with state (3) seen in *Arribasuchus* and *Pseudopalatus*, in part 2.3.4.1, (6).

Character 28 is essentially a character complex that covers a number of features that have been treated separately in previous studies. It includes the size and shape of the supratemporal fenestra (CAMP 1930; GREGORY 1962a; BALLEW 1989: characters 16a, b; 17a, b; LONG & MURRY 1995), and in parts the width of the postorbito-squamosal bar (BALLEW 1989: character 34; MURRY & LONG 1989; LONG & MURRY 1995). The presence of a moderate to strong medial lamella (states 2 and 3) probably coincides with the feature of the postorbito-squamosal bar being very wide, defined as being "not longer than six times its width", which was used to characterise Pseudopalatinae (MURRY & LONG 1989; LONG & MURRY 1995). Since forms like both species of *Mystriosuchus* without well developed medial laminae of the squamosals also show wide postorbito-squamosal bars, this character is treated here separately (character 20).

It is frequently stated that it is the progressive depression of the parieto-squamosal bar in phytosaurs that results in a concealment of the supratemporal fenestra in dorsal view (BALLEW 1989: character 16b; LONG & MURRY 1995: 57; HUNT & LUCAS 1993b: 193). *Mystriosuchus* demonstrates clearly, however, that even the maximum depression observed in a phytosaur does not necessarily lead to a "concealed", i.e. significantly covered or narrow supratemporal fenestra in dorsal view. Similarly, there is no apparent reason why the shape and orientation of the squamosal process of the parietal should lead, *a priori*, to invisibility of the process in dorsal view, as claimed elsewhere (BALLEW 1989: characters 17a, b). The actual width of the supratemporal fenestra, and hence the section of the parieto-squamosal process which is exposed in dorsal view, is in fact negatively correlated with the development of a medial extension of the squamosal, and depends on this feature alone. The only exception seems to be SMNS 12593, in which the exposure of the supratemporal fenestra (the posterior part only) is reduced by the

orientation of the squamosal processes of the parietal. *Nicrosaurus* species B was not considered in the study quoted above. A character combination of depression of the parieto-squamosal bar with the closure of the dorsal aperture of the supratemporal fenestra is unjustified and results only in confusion.

(29) height of the lateral vertical part of the squamosal: shallow, less than one third of skull height (0) - high, equally or more than one third of skull height (1)

The squamosal body and the posterior process in lateral view is primitively shallow in the outgroups, all non-phytosaurid phytosaurs, *Rutiodon*, *Nicrosaurus*, *Arribasuchus*, *Pseudopalatus*, which achieve a height of less than one third of the skull height at best (state 0). Both species of *Leptosuchus*, and *Smilosuchus gregorii* show a considerably higher lateral aspect of the squamosal that well exceeds this figure (state 1). The height increase is not restricted to the squamosal body, but is especially well-developed on the posterior process (CAMP 1930). The lateral plane of the squamosal shows a maximum development in *Leptosuchus* crosbiensis, in which the posterior process reaches more than half the height of the skull (BALLEW 1989: character 24). The lateral face of the squamosal is also enlarged in *Angistorhinus* and *Brachysuchus* (MEHL 1916, 1922; DUTUIT 1977a; CASE 1929).

(30) development of the posterior process of the squamosal: absent (0) - present, but short (1) - moderate, c. 10 to 50 mm (2) - long, > 50 mm (3)

(30[1]) absent (0) - present (1)

(30[2]) absent, or short (0) - moderate to long, > 10 mm (1)

(30[3]) absent, or short to moderate, ≤ 50 mm (0) - long, > 50 mm (1)

There are contradictory statements in the literature about the presence and length of the posterior process of the squamosal in the various taxa. The confusion probably has its roots in several reasons: firstly, in differing opinions on what actually constitutes a posterior process, secondly, in the presence and length of the process depending on whether the tip of the squamosal lies at the level of or behind the extremity of the quadrate (here character 31), and, thirdly, the condition is confused by the usage of imprecise morphological terms that have frequently been adopted to describe the length of the process (e.g. "truncated squamosal", GREGORY 1962a,b; BALLEW 1989; HUNT & LUCAS 1989b; LONG & MURRY 1995).

The posterior process of the squamosal is here redefined as a posterior extension of the dorsal and lateral surface of the squamosal beyond the insertion of the parieto-squamosal bar with the medial side of the squamosal body. According to this definition, a

posterior process is absent (state 0) in *Mystriosuchus* species B (part 3.3.2.1) and the majority of non-phytosaurid phytosaurs. A short process extending somewhat behind the parieto-squamosal bar (state 1) is present in *Paleorhinus bransoni*, *Paleorhinus magnoculus*, *Francosuchus* (in contrast to the statement in BALLEW 1989: character 12a), the angistorhinine *Brachysuchus*, and *Mystriosuchus planirostris* (subsection 3.2.2). The term moderately long (state 2) is used to describe a process length up to approximately 50 mm, which is present in *Angistorhinus*, *Leptosuchus*, *Smilosuchus*, *Rutiodon*, and *Nicrosaurus*. State (2) seems to represent the "standard" length within basal Phytosauridae. A posterior process of the squamosal exceeding the figure of 50 mm (state 3) is found in *Leptosuchus crosbiensis* (LONG & MURRY 1995), and considerably elongated squamosals than this figure in *Arribasuchus buceros* and *Pseudopalatus pristinus* (BALLEW 1989).

(31) extent of the squamosal: terminates in front of, or at level with, the posterior rim of the quadrate (0) - overhangs the posterior rim of the quadrate (1)

This character is introduced to determine whether the squamosal extends beyond the posterior edge of the quadrate, which is naturally the case in all taxa showing moderate and long posterior processes. Note, however, that the tip of the squamosal may reach beyond the level of the quadrate in taxa in which no posterior process according to the definition above is present (*Paleorhinus scurriensis*, "*Parasuchus hislopi*", *Brachysuchus megalodon*). The presence of the derived character state is thus independent from the lack or the presence of a very short posterior process.

(32) tip of the squamosal in dorsal view: tapering to pointed or a subpointed tip (0) - broadly rounded tip (1)

The polarity of the character transformation is polarised by the pointed squamosal tip of *Euparkeria*. Actually, no phytosaur shows such an acute tip, but in numerous taxa the squamosal tapers to various degrees with straight medial and lateral rims and can hardly be described as rounded (non-phytosaurid phytosaurs except *Ebrachosuchus* and *Paleorhinus magnoculus*, *Leptosuchus crosbiensis*, *Smilosuchus*, *Arribasuchus*, and *Pseudopalatus*). Such a condition is termed subpointed. BALLEW (1989: character 41, in parts) postulated a not rounded squamosal tip corresponding to my character state (0) as synapomorphic of a clade including *Arribasuchus*, *Pseudopalatus* and *Mystriosuchus*. I feel that BALLEW intended to apply the character states to phytosaurs with posterior processes of the squamosals only, but the tips of the squamosals are the same homologous structures regardless of the presence or absence of a posterior process, and must therefore be scored as pointed as well. The primitive character state includes also

squamosals with angular medial rims (*Nicrosaurus* species B, part 2.3.4.1, (2) and (5)) and sigmoidal medial rims (*Mystriosuchus planirostris*, subsection 3.2.2) that both end in subpointed tips.

The derived broadly rounded squamosal tip (state 1) is present in the outgroup *Proterochampsa*, all Angistorhininae, *Nicrosaurus kapffi*, *Leptosuchus adamanensis*, and *Rutiodon carolinensis*.

(33) depression of the parieto-squamosal bar: absent (0) - slightly below the skull roof (1) - moderate to strong depression, 15% to 25% of skull height (2) - very strong depression, more than 25% of skull height (3); see Appendix B, Table B.5

(33[1]) absent (0) - present (1)

(33[2]) absent, or slightly depressed (0) - moderate to very strong depression, ≥ 15% skull height (1)

(33[3]) absent, or slight to strong depression, ≤ 25% skull height (0) - very strong depression, > 25% skull height (1)

The depression of the parieto-squamosal bar below the level of the skull roof is unique to advanced phytosaurs among archosaurs, and has always been reckoned one of the most important characters in phytosaur phylogeny (e.g. GREGORY 1962a; BALLEW 1989: character 15, in parts).

The posterior border of the supratemporal fenestra is essentially level with the skull roof bones (state 0) in almost all non-phytosaurid Phytosauria, *Brachysuchus*, and *Angistorhinus*. Differing accounts for *Paleorhinus bransoni* (CASE 1922) and *Brachysuchus* (CASE 1929) are now unanimously recognised as *post-mortem* effects caused by crushing (MEHL 1915; GREGORY 1962a; LONG & MURRY 1995). However, GREGORY (1962a) and MURRY (1986) stress that in *Paleorhinus scurriensis* the parieto-squamosal bar is somewhat lowered with respect to the skull roof. This condition was coded as state (1), although the degree of depression cannot be established because of incomplete preservation of the type specimen (LANGSTON 1949: fig. 1), and the deeper position of the bar might represent a preservational artefact.

In the more derived taxa, the degree of depression is quantified here for the first time, based on my own data from *Nicrosaurus* and *Mystriosuchus*, and data from figured specimens (Tab. B.5). It is apparent that deformation plays a role in the variation seen within an OTU with a relatively high number of entries (*Nicrosaurus kapffi*, *Mystriosuchus planirostris*). For instance, the most extreme value for *Mystriosuchus planirostris* (38%) is derived from the laterally compressed skull SMNS 10260.

Secondly, within genera and species, relatively increased skull height leads to lower percentages (e.g. *Leptosuchus crosbiensis*; high-domed and low-domed morphs of *Nicrosaurus kapffi*). Nevertheless, two clusters are discernible: the first comprises *Leptosuchus*, *Smilosuchus*, and *Nicrosaurus* with values between 15 and about 25% (state 2). *Pseudopalatus*, *Arribasuchus*, and *Mystriosuchus* all exceed this value with *Mystriosuchus planirostris* scoring by far the highest figures although having a comparatively very high skull (state 3). This character transformation series is congruent with the taxonomic hierarchy resulting from the analysis, and suggests an evolutionary trait of opening the supratemporal fenestra posteriorly. No exact figure is available for *Rutiodon carolinensis*, and the taxon has been tentatively coded 2. The specimens referred to *Rutiodon carolinensis* show extensive deformation in the supratemporal area (GREGORY 1962b) or the region is very incompletely preserved (DOYLE & SUES 1995). GREGORY (1962b: 9, fig. 3) reconstructed the parieto-squamosal bar as a straight, but constantly declining strut rather than levelling out in its lateral part, suggesting an intermediate condition between the states (0, 1) and (2). However, I suspect that this is based on a preservational artefact because the figured fragment is laterally compressed. A similar sloping parieto-squamosal bar could be reconstructed for *Nicrosaurus kapffi* based on the laterally deformed SMNS 54706 (Fig. 2.21).

(34) shape of the parieto-squamosal bar: essentially straight in dorsal view (0) - arches broadly posteromedially (1)

The character is adopted from LONG & MURRY's (1995) diagnosis of Angistorhininae. In this group, represented here by *Brachysuchus megalodon*, *Angistorhinus grandis*, and *Angistorhinus talainti*, the medial rim of the parieto-squamosal bar (and the posterior process of the squamosal) form a distinctly rounded arc that is convex in posteromedial direction when seen from above (state 1). In all other taxa, the parieto-squamosal bar closing the supratemporal fenestra posteriorly is more or less straight.

(35) length of the quadratojugal process of the squamosal: short, forms ≤ 50% of the posterior rim of the infratemporal fenestra (0) - long, forms > 50% of the posterior rim of the infratemporal fenestra (1); see Appendix B, Table B.6

The character is polarised by the comparatively short quadratojugal process in *Euparkeria* (c. 40%), which is further substantiated by a tiny process visible in other crurotarsans (e.g. WALKER 1961, 1990). In phytosaurs, the length of the quadratojugal process of the squamosal is actually an indicator of the anterodorsal extent of the

quadratojugal in lateral view, because this bone covers large parts of the process externally.

A short process is retained only by *Paleorhinus magnoculus*, *Promystriosuchus ehlersi*, *Smilosuchus gregorii*, *Nicrosaurus kapffi*, and *Arribasuchus buceros*. The process being not visible at all along the infratemporal fenestra of *Paleorhinus magnoculus* reflects the unusual size and shape of the quadratojugal in this species. It is also noteworthy that among Phytosauridae all particularly robust forms with tripartite dentitions retain the shorter process, which might be explained by a higher resistance of a large, overlapping cheek suture to stress and torsion that must have occurred in that area during feeding.

(36) paroccipital process of the squamosal: tiny, does not extend below the paroccipital process of the opisthotic (0) - well developed, extends below the opisthotic (1)

A paroccipital process of the squamosal, when defined as a posteriorly or ventrally directed, discrete extension of the squamosal supporting the paroccipital process of the opisthotic, is actually present not only in phytosaurs (SERENO 1991) or a synapomorphy of Phytosauridae (BALLEW 1989: character 10), but is much more widespread among crurotarsans (see subsection 5.4.1). In a number of primitive phytosaur taxa (*Ebrachosuchus*, *Francosuchus*, *Paleorhinus magnoculus* and *Paleorhinus sawini*, and *Promystriosuchus*), the process is present, but remains as tiny as in most other crurotarsans. It is only in the remaining non-phytosaurid phytosaurs (figured for "*Parasuchus hislopi*", CHATTERJEE 1978, *Paleorhinus bransoni*, LEES 1907, and noted by MURRY 1986 for *Paleorhinus scurriensis*) and Phytosauridae that the process is developed to a prominent structure that extends markedly ventral to the paroccipital process of the opisthotic (state 1).

(37) length of the supraoccipital shelf: short, predominantly vertical (0) - posteroventral part horizontally deflected (1) - elongated, with extended horizontal component (2)

(37[1]) short, predominantly vertical (0) - posteroventral part horizontally deflected (1)

(37[2]) short, or short horizontal deflection (0) - deflected part elongated (1)

Although character 37 is variable among phytosaurs, it is only included in the data matrix pending further investigation because there are difficulties in distinguishing precisely between the character states (1) and (2). The entries for the remaining taxa are based on published figures of skulls in dorsal view, and the scores need to be checked in

the actual specimens. Only *Nicrosaurus* and *Mystriosuchus* have been scored by personal observation.

In the outgroups, and all other Crurotarsi, the supraoccipital is essentially a vertical plate of bone and thus almost invisible in dorsal view (state 0). This primitive condition is also illustrated for *Paleorhinus bransoni*, *Paleorhinus sawini*, "*Parasuchus hislopi*", and the Angistorhininae. Character state (1) was scored for taxa, in which there is a distinct horizontal deflection of the supraoccipital shelf visible in dorsal view. This is figured for *Ebrachosuchus*, *Francosuchus*, *Mesorhinosuchus*, *Promystriosuchus*, and *Paleorhinus magnoculus* and *Paleorhinus scurriensis* among primitive phytosaurs, as well as in *Leptosuchus*, *Smilosuchus*, and *Rutiodon*. Similarly, the high supraoccipital complex of *Mystriosuchus* matches this definition. *Nicrosaurus*, *Arribasuchus*, and *Pseudopalatus* show a parietal-supraoccipital complex in which the horizontal component is elongated, resulting in a deeper trough-like appearance of the shelf (state 2). Although differences have been noted regarding the length of the deflected part of the supraoccipital shelf between *Nicrosaurus kapffi* and *Nicrosaurus* species B (see subsection 2.3.3), and the same part seems to be more elongated in *Arribasuchus* and *Pseudopalatus*, these differences are difficult to quantify and state (2) is not further subdivided.

(38) lateral extent of the supraoccipital: forms the dorsomedial border or touches the medial corner of the posttemporal fenestra (0) - does not contribute to the posttemporal fenestra (1)

(39) paroccipital process of the opisthotic: dorsal and ventral rims parallel or slightly diverging (0) - lateral part significantly enlarged (1)

Both outgroups and all non-phytosaurid phytosaurs possess a paroccipital process of the opisthotic that is only insignificantly enlarged laterally and thus appears as a fairly slender strut appressed to the squamosal (state 0). In all Phytosauridae, by contrast, the lateral half of the paroccipital process shows a considerable increase in height, and therefore terminates as a broad and massive plate (state 1). As demonstrated by *Nicrosaurus* and *Mystriosuchus*, this is largely achieved by the development of a ventral opisthotic ridge. The actual shape of the enlarged section of the paroccipital process, whether developed as a discrete "oar-shaped", subrectangular structure or as a continuously enlarged extremity of the process, may vary within a species (see part 2.2.5.2).

(40) size of the quadrate foramen: large (0) - reduced (1)

According to *Euparkeria*, a large quadrate foramen is the plesiomorphic condition (see subsection 5.4.1, (16)). *Ebrachosuchus*, *Francosuchus*, *Paleorhinus bransoni*, and *Paleorhinus sawini* retain a comparatively large quadrate foramen (state 0). The foramen is especially large in *Mystriosuchus*, although there are minor differences in size and shape between both species (part 3.3.4.2, (5)). In the remaining non-phytosaurid phytosaurs and Phytosauridae, the lumen of the quadrate foramen is considerably reduced (state 1) to about half the size of the primitive state.

(41) position of the quadrate foramen: visible in lateral and posterior view (0) - visible in posterior view only (1)

In the outgroups, the species referred to *Paleorhinus*, and "*Parasuchus hislopi*", the quadrate foramen is apparently not located in a deep recess between the quadrate and the quadratojugal, and therefore visible in both posterior and lateral view of the skull (state 0). A sharp lamella of the quadratojugal is developed in the derived state (1) that obscures the quadrate foramen when seen from the side.

(42) dimensions of the posttemporal fenestra: dorsoventrally wide (0) - dorsoventrally narrow (1)

See discussion in part 3.1.2.1.

(43) premaxilla reaches the choana: absent (0) - present (1)

Most taxa included in the analysis show the plesiomorphic condition with the palatal process of the premaxilla terminating in front of the choana (state 0) as in *Euparkeria* and all other crurotarsans. In *Ebrachosuchus*, *Paleorhinus scurriensis*, *Angistorhinus talainti*, *Leptosuchus crosbiensis*, *Rutiodon carolinensis*, and *Mystriosuchus planirostris* (according to MCGREGOR 1906, no recent data available), the premaxilla participates in bordering the choana anteriorly (state 1). The character seems to be polymorphic in *Smilosuchus* (CAMP 1930; COLBERT 1947). The derived state is negatively correlated with the length of the prechoanal part of vomers. It may lead in extreme cases to the premaxilla contacting the palatine and excluding the maxilla from the anterior border, a condition that has not been coded separately.

However, it has been pointed out above (subsection 2.1.2; part 2.2.3.3) that the prechoanal part of the palate is frequently imperfectly preserved or the configuration is difficult to interpret, and a reinvestigation of all taxa might lead to different interpretations

and character distributions. Character 43 is thus tentatively incorporated in the data matrix, and needs further investigation.

(44) anterior extent of the palatine: behind the choana or forming the posterior rim (0) - terminates posterior to the anterior rim of the choana (1) - reaches level of the anterior rim of the choana (2) - extends forward beyond the anterior rim of the choana (3)

(44[1]) terminates behind the posterior rim of the choana (0) - terminates in front of the posterior rim of the choana (1)

(44[2]) terminates behind the anterior rim of the choana (0) - terminates at level or in front of the anterior rim of the choana (1)

(44[3]) terminates behind to at level of the anterior rim of the choana (0) - terminates in front of the anterior rim of the choana (1)

Primitively, in basal archosaurs and crurotarsans the palatine lies far behind the choana, or may form the posterior and posteromedial border at best (state 0, CHARIG & SUES 1976; EWER 1965; WALKER 1961, 1964, 1990). In phytosaurs, there is a trend for the palatine to extend forward along the lateral rim of the choana, restricting progressively the contribution of the maxilla to the choanal rim. However, in contrast to SERENO (1991), the palatine does not form the entire lateral border of the choana in all taxa, but remains distinctly behind in *Ebrachosuchus*, *Francosuchus*, and *Mesorhinosuchus*. This condition is defined as state (1). Further progressive states are the palatine terminating about level with the anterior rim of the choana (state 2), and extending significantly forward beyond (state 3). In several taxa the scoring is tentatively (indicated by "(?)" in the data matrix, Appendix A) because the anterior extent of the palatine is reconstructed. The character state in *Pseudopalatus* remains unclear because of the incorrect configuration of the palate shown in MEHL (1928b).

(45) medial extension of the palatines: absent, palatines restricted to the vertical part of the palatal vault (0) - present, palatines extend onto the roof of the palatal vault and are visible in ventral view (1)

According to the published illustrations, the pterygoid forms the entire roof of the palatal vault in most phytosaurs, and the medial wing of the palatine is not visible when seen from below. The outgroups do not show a palatal vault, and the predominant occurrence of this configuration among the most primitive taxa included in the analysis suggests that this is the plesiomorphic character state (0). The medial wing of the palatine is extended in *Paleorhinus bransoni*, *Paleorhinus scurriensis*, and *Leptosuchus*

crosbiensis, and thus appears on the roof of the palatal vault in ventral view (state 1). The largest extension of the palatines is seen in *Nicrosaurus* (next character).

(46) palatines meet in midline of the palatal vault: absent (0) - present (1)

See discussion in subsection 2.1.2.

(47) shape and number of the suborbital fenestrae: anteroposteriorly elongated and wide singular fenestra (0) - singular fenestra reduced in width (1) - singular fenestra reduced in length, or subdivided in two or more fenestrae (2); see Appendix B, Table B.7

According to the outgroups, the primitive character states (0) of the suborbital fenestra are: one fenestra present, which is anteroposteriorly elongated (polarity *contra* MURRY 1989: 125), comparatively broad, with the maxilla contributing to the anterior rim. *Mesorhinosuchus* retains a broad supratemporal fenestra compared to all other Phytosauria. Within phytosaurs, the suborbital fenestra is progressively reduced in size. State (1) represents a reduction in width to a narrow slit-like opening. The singular elongated suborbital fenestra is somewhat wider in *Ebrachosuchus*, *Francosuchus*, "*Parasuchus hislopi*", and especially in *Brachysuchus* than in the other taxa that are scored as (1), but the reduction in width seems to be gradual and it is difficult to recognise discrete character states. Further reduction takes place in different traits, which all result in a reduction in length of the suborbital slit and thus can be summarised as state (2). The first trait (2a) is a reduction of the slit to a single, small, oval opening. This condition correlates well with the maxilla losing contact with the reduced opening. In trait (2b) the slit is subdivided into two or more separate smaller openings (demonstrable as an ontogenetic trait in *Nicrosaurus kapffi*, see part 2.2.7.1). The posterior fenestra corresponds in size (except in *Paleorhinus scurriensis*, LANGSTON 1949), topology, and topography to the single reduced opening of trait (2a). The anterior opening is always smaller, but no constant pattern of the palatal bones surrounding this fenestra is discernible. DUTUIT (1977a: 309; pl. 1 fig. D, pl. 2 fig. B) describes a small recess between the maxilla and the palatine of *Angistorhinus talainti* in the approximate position of a suborbital fenestra, but not an opening, and there is no suborbital fenestra indicated in his reconstruction (DUTUIT 1977a: fig. 2B). The apparent complete loss of the suborbital opening in this species is interpreted as trait (2c) and might be a result of the widely diverging posterior palatine ridges and the only minutely bulging maxillae of this species, which narrows the palatal plane considerably. The distribution of these traits among the OTUs is indicated in Table B.7. The transformations among the character

states 0, 1, and 2 on the cladogram Figure 5.5 show no hierarchical discordance, and support the suggestion of a linear, albeit often reversed transformation series.

(48) length of the interpterygoid vacuity: long, more than 50% of the distance between the choana and the posterior rim of the palatal vault (0) - shorter than 50% (1) - tiny oval indentation (2)

(48[1]) long, more than 50% of the distance between the choana and the posterior rim of the palatal vault (0) - moderately long, shorter than 50% (1)

(48[2]) long to moderately long slit (0) - tiny oval indentation (1)

The cleft separating both pterygoids is broad and long in the outgroups. In all phytosaurs, the width of the interpterygoid vacuity is reduced, but *Ebrachosuchus*, *Francosuchus*, *Paleorhinus ehlersi*, *Angistorhinus grandis,* and even *Rutiodon carolinensis* still retain the plesiomorphically long condition (state 0). A reduced length to less than half the length of the palatal vault, defined as state (1), and the restriction to a tiny oval indentation of the posterior rim of the palatal vault (state 2) occur disparate among the remaining taxa. However, the distribution should be checked in the specimens, because the interpterygoid suture in e.g. *Nicrosaurus kapffi* runs in a groove on the palatal vault, which is not always freed from matrix and on superficial examination might easily be mistaken as an infilled slit. The most derived state is by no means restricted to more derived phytosaurs as suggested by GREGORY (1962a), but is not uncommon even among non-phytosaurian phytosaurs (*Paleorhinus bransoni*, *Paleorhinus scurriensis*, "*Parasuchus hislopi*").

(49) position of the foramen (foramina) nervi hypoglossi: on the lateral face of the exoccipital pillar (0) - located in the jugular recess (1)

See discussion in subsection 2.1.2.

5.3.2 Characters excluded from the analysis

5.3.2.1 Intraspecifically variable characters states

A number of characters have been found that are variable within the species *Nicrosaurus kapffi* and *Nicrosaurus* species B. It may be assumed that such characters, which are polymorphic in well established morphospecies, are likely to be variable in other OTUs as well. A number of different methods have been suggested to deal with

polymorphic data in a parsimony analysis, and a method coding the frequency in an unfixed character was found to perform best to extract an inherent phylogenetic signal (WIENS 1995). In the majority of taxa included in the analysis, intraspecific variants are rarely described giving the impression to be absent, or the small number of specimens known does not allow determination of character variability. Furthermore, WIENS substantiated the view that intraspecific variability is significantly and positively correlated with homoplasy, and thus such characters are less reliable to contain phylogenetic information. I have chosen to avoid employing characters that are polymorphic within an OTU whenever possible.

Characters that found here to be intraspecifically variable are listed in Table 2.2.10 and are discussed in subsection 2.2.7 and part 2.3.4.2. Historically the most important character complex excluded in the cladistic analysis is the relative height or relative width of the skull, which has been used widely in the form of height to width ratio of the skull in occipital aspect or the height of the quadrate to define categories above species levels (GREGORY 1962a, CHATTERJEE 1978; LONG & MURRY 1995). This includes also correlated features like the slope of the cheek (BALLEW 1989: characters 22, 28), the orientation of infratemporal fenestra, and the orientation of the orbits (BALLEW 1989: character 6; LONG & MURRY 1995). A second important complex is the presence or absence of a partial prenarial crest, as well as morphological details of the prenarial crest, which appear frequently in BALLEW's analysis (1989: characters 21 [partim], 26, 32, 56, and 57 [partim]). Since this character complex is variable in *Nicrosaurus* species B, it was neglected in the present analysis. A character not treated so far is the reduction of the internal antorbital opening suggested as characteristic for more advanced phytosaurs (WITMER 1997), which is actually individually variable in *Nicrosaurus* species B and probably also in *Rutiodon carolinensis* according to data from GREGORY (1962b) and DOYLE & SUES (1995).

5.3.2.2 Imprecisely phrased and poorly defined character states

In some cases, I found it difficult to understand the meaning of characters suggested in previous analyses or descriptions. A number of such ambiguous character definitions have been discussed in the descriptive parts of this study. A rephrasing as in the case of characters 4, 5, 16, 18, 20, 22, 23, 30, and 47 in this study resulted in more clarity, however, some characters need to be re-investigated with the specimens at hand. These include in particular

- the "compressed" squamosals (BALLEW 1989: characters 12b, 41, 62 [partim])
- the overhang of the squamosal process of the parietal over the supraoccipital shelf (BALLEW 1989: character 42; character 27 of this study)
- the length of the supraoccipital shelf (character 37 of this study)
- the width of the palatal vault (KUHN 1936)

In a large group of characters, the character states form a morphocline, so that it is difficult or impossible to decide on the basis of their pattern of distribution how two (or more) character states could be defined. A few metric and numeric characters with arbitrarily chosen characters states are included in the analysis (1, 6, 20), however, this is hardly possible with morphologically defined (qualitative) characters. Further ambiguity is added, when these characters are prone to be affected by *post-mortem* deformation. The list below is by no means complete, but only quotes a selection of such characters assessed to be phylogenetically significant by previous authors.

- the shape of the antorbital and the infratemporal fenestra (e.g. BALLEW 1989: character 61; HUNT & LUCAS 1989b; see discussion in *Mystriosuchus* species B, part 3.3.4.3, (iv))
- the length of the squamosal body, i.e. the length of the aperture of the tympanic fossa (see *Nicrosaurus* species B, part 2.3.4.1; also employed to subdivide Angistorhininae by LONG & MURRY 1995)
- the degree of the divergence of the squamosal processes of the parietals (see discussion for *Nicrosaurus* species B, part 2.3.4.1)
- the morphology of the "parietal extensions", which probably corresponds to the squamosal processes of the parietals (BALLEW 1989: characters 18a, 18b)
- the detailed shape of the posterior process of the squamosal (CAMP 1930)
- the width of the posttemporal fenestra (BALLEW 1989: characters 8, 20, 30, 46, 49, 54)
- the shape and inclination of the quadrate (GREGORY 1962a; CHATTERJEE 1978)
- the development of ridges on the basioccipital (HUENE 1911, 1922)

Numerous additional examples of characters, which have never been used to reconstruct the phylogeny of phytosaurs before but need to be investigated, are listed in Table 2.3.4.

5.3.2.3 Characters showing discrete states, but poorly known distribution

In this category, I group characters in which discrete character states are either determined in this study or seem to be present according to published descriptions of single specimens. The data is, however, largely unavailable for the great majority of taxa included, so that informativeness of the character distribution is at present very limited. However, these characters have the potential to be incorporated in the data matrix after further investigations.

- braincase characters: These include the proportional length of the central stem, the morphology, orientation, and individuality of the basal tubera, the position of nerve and vessel foramina, and the presence or absence of individual braincase components
- palate and palatal vault: the extend of vomers and premaxillae, and shape and morphology of the palatines, including the development of rugosities or ridges (CASE 1922; see also *Nicrosaurus* species B, subsection 2.3.3)
- occipital aspect of the skull: the configuration of, and connectivity among, individual elements, and details of the paroccipital process like orientation of its posterior surface, the morphology of the cristae, and anteroposterior thickness
- morphology of the teeth, after exclusion of these characters which are subjects to positional and ontogenetic variation (see subsection 2.2.5)

Section 5.4
Phylogenetic analysis

5.4.1. Data matrix and methods

5.4.1.1 The data matrix

A data matrix including 24 OTUs, two of which are outgroups, and 49 characters is presented in Appendix A. The data matrix contains 16 multistate characters (33% of the total). In the cases of inapplicable characters in *Euparkeria* (characters 3, 7-8, and 45) and *Proterochampsa* (the same, plus characters 38 and 40 - 42), the state is coded as such ("n/a"), being treated as unknown ("?") in the analysis. Out of 1176 entries, 13 data

points (1.1%) do not apply and for a further 103 data points (8.6%), the character state is unknown, resulting in a total of approximately 10% of missing data. Three taxa show a substantial amount of missing data (*Mesorhinosuchus*, 20 missing data points; *Paleorhinus sawini*, 20 missing data points; *Rutiodon carolinensis*, 10 missing data points). However, the software programme TAXEQ that identifies such taxa, the character states of which are fully replicated in another, and thus can be safely deleted from the data matrix (safe taxonomic reduction: WILKINSON 1992b, 1995; WILKINSON & BENTON 1995), failed to find redundant OTUs. Similarly, deleting of the OTUs showing a large quantity of missing data did not result in a reduction in tree numbers or a substantial better resolution of the remaining taxa.

5.4.1.2 Methods

Invariant settings of the parsimony analyses

Several parsimony analyses were conducted using the software programme PAUP 3.1.1 (Phylogenetic Analysis Using Parsimony, SWOFFORD & BEGLE 1993) run on a PowerMac computer to produce the most parsimonious branching pattern. The invariable settings of the parsimony analysis are as follows: all searches for most parsimonious trees (MPT) were heuristic, using the options "collapse zero-length branches", branch swapping by "TBR branch-swapping" with "steepest descent" activated, starting trees obtained by "stepwise addition", the addition sequence being "random", and 100 replications performed. When computing tree lengths, multiple states in a OTU were treated using the option "polymorphism", which resulted, on the basis of the data matrix given, in tree lengths increased by 4 steps in comparison to the option "uncertainty". Character state transformations were optimised in the reconstruction of transformations of ambiguous (homoplastic) characters on the trees using "delayed character transformation" (DELTRAN), which results in parallel evolution being preferred over reversals (as favoured by employing the algorithm "accelerated character transformation", ACCTRAN). This is based on the assumption that parallelisms are more likely to have occurred in the evolutionary history of phytosaurs than reversals, although it is acknowledged that ACCTRAN is superior from a theoretical point of view (PINNA 1991). DELTRAN also reduces the likelihood that character transformations assigned to interior nodes are not supported by the actual data in the terminal OTUs (SMITH 1994). The trees were rooted by outgroup rooting using *Euparkeria* and *Proterochampsa*.

To evaluate the support of the individual branches of the MPTs resulting from the analyses, two methods are employed. Firstly, a bootstrap analysis was performed (1000 replications; search settings: heuristic, stepwise addition, addition sequence simple). The per cent distribution of a clade among the resulting MPTs of all replications provides a cautious estimate of the probability whether the initial analysis has identified this clade correctly (SMITH 1994). Secondly, a number of subsequent runs were performed, in which several constraints were enforced upon the MPTs retained by the parsimony analysis. Such constraints include clades or groupings of terminal taxa that are not present in the MPTs of the initial analysis, but have been hypothesised by previous workers. The minimum number of additional steps required to produce such suboptimal trees when compared to the MPTs without the constraint is then used as a relative measurement for the probability, how far the constraint clades represent a reasonable option to be considered in reconstructing phytosaur phylogeny.

Analytical runs and variable settings

In the initial analysis, all multistate characters were left unordered. This run resulted in five MPTs, each of which shows a length of 190 steps. The overall consistency index (CI) of each of these trees is 0.400, the rescaled consistency index (RCI) is 0.227, and the retention index (RI) is 0.567. The comparatively small amount of missing data in the data matrix suggests that these low indices are largely the result of homoplastic distribution of character states. The minimum phylogenetic information contained in these five trees was summarised by calculating a majority consensus tree, which is presented in Figure 5.3.

A second analysis was performed, in which the transformation series of the multistate characters 1, 6, 10, 16, 18, 20, 24, 28, 30, 33, 37, 44, and 48 were treated as ordered, but reversible (WAGNER parsimony). Each of these characters represents by its definition a morphocline, and the similarity criterion (LIPSCOMB 1992; "method of intermediates", WILKINSON 1992a) combined with the polarity as defined by outgroup comparison suggests that the character state transformation is linear and conform with ascending character state designations. This is based on the assumption that a character being transformed from e.g. state 0 to state 2 must necessarily pass the intermediate state 1. Thus, the transformation should be counted as two steps, in contrast to one step of the similar transformation of the unordered character. This in turn influences the calculation of the most parsimonious branching pattern, and may affect the tree topology compared to that from the initial unordered analysis. *A priori* ordering of multistate characters is not generally accepted, because it can result in differential weighting of some of these

characters (HAUSER & PRESCH 1991, and references therein). A justification of such linear-ordered transformations, however, is provided by WILKINSON (1992a), who argued that the use of ordered and polarised multistate characters is consistent with HENNIG's auxillary principle (saying that apomorphous similarity should primarily be regarded as evidence for phylogenetic relationship, rather than for homoplasy), and has a greater explanatory power in offering an explanation for the observed similarity. The characters 5, 15, and 47, for which similarity does not suggest *a priori* a particular character state tree, were left unordered. This analysis resulted in 35 MPTs with the greater length of 203 steps, showing a CI of 0.374, a RCI of 0.225, and a RI of 0.602. A consensus tree (50% majority rule) of this analysis is shown in Figure 5.4.

To compare the quality of the results of both analyses, a new analysis employing the same character ordering was run, however, enforcing the constraint that only trees compatible with the trees resulting from the previous unordered analysis should be retained. It was found that under this setting producing the same trees as with unordered characters requires 206 steps, i.e. 4 steps more. For this reason, and for the position of *Rutiodon carolinensis* congruent with previous phylogenetic hypotheses (see below), the result of the analysis using ordered multistate characters is regarded as more reliable.

Judged by the criterion of parsimony, all 35 MPTs are optimal and similarly likely to represent the true relationship among Phytosauria.

There is no tree among the 35 MPTs that matches exactly the consensus tree (50% majority rule) in Figure 5.4. Two other methods incorporating differential weighting were tried to choose among the MPTs obtained. The essential branching points of the resulting trees derived by each method were captured by a strict consensus tree, which was compared with the trees recovered by the analysis with ordered multistate characters. Only those trees among the 35 MPT that match this constraint strict consensus tree recovered by *a posteriori* weighting were selected, and these trees were used to describe the character state transformations for the subclades in subsection 5.4.3.

Firstly, an additional parsimony analysis was performed based on a data matrix in which the 14 ordered multistate characters of the previous analyses have been transformed into sets of additive binary characters. Effectively, this results in an arbitrary *a priory* high-weighting of these characters. This run yielded the substantially less number of 2 MPTs with 202 steps. However, both these MPTs are not included among the 35 trees of the previous analysis, and were thus discarded.

Secondly, a number of runs were undertaken with successive approximations character weighting. In this method, the analysis starts with equally weighted characters, and the characters are reweighted *a posteriori* according to a measurement of fit as

determined by the previous run, and the data is then reanalysed. Reweighting and reanalaysing continues until the weight no longer changes or identical trees are found in a consecutive run (SWOFFORD & BEGLE 1993). As measurement of fit, both RCI and CI were chosen (when these vary among the trees in subsequent runs, the option was set to "average fit"; for reasoning, see WILKINSON & BENTON 1995), and the baseweight was set to 3. Thus, character incongruences are expected to be resolved by successively low-weighting of homoplastic characters. Only successive character weighting according to RI and CI produced trees, among others, that where found among the 35 optimal MPTs: CI resulted in trees 10, 25, and 26, and RI reproduced tree 10. Tree 10 in particular was selected as basis for identifying character transformations, and is illustrated in Figure 5.5.

5.4.2 Description of the MTPs

Majority rule consensus tree from the analysis with all multistate characters unordered (Fig. 5.3): *Paleorhinus sawini* is identified as the most primitive phytosaur. *Paleorhinus magnoculus*, *Mesorhinosuchus fraasi* + *Promystriosuchus ehlersi*, and *Ebrachosuchus neukami* + *Francosuchus angustifrons* branch off successively. "*Parasuchus hislopi*", and *Paleorhinus bransoni* + *Paleorhinus scurriensis* are found to be the most derived primitive phytosaurs, forming a trichotomy with Phytosauridae. The Phytosauridae (as defined by DOYLE & SUES 1995) constitute a monophyletic group, but the ingroup relationships are only partially resolved. In all trees, *Rutiodon carolinensis* is identified as the sistergroup to all other Phytosauridae, and is thus, in contrast to all previous studies, assessed as more primitive than both *Angistorhinus* and *Brachysuchus*. The more derived Phytosauridae are arranged in a polychotomy including *Leptosuchus crosbiensis*, *Leptosuchus adamanensis*, *Smilosuchus gregorii*, the clade Angistorhininae, and a clade formed by the remaining Phytosauridae. There is no definite resolution among the OTUs of Angistorhininae. The most derived subclade of Phytosauridae present in all MPTs is represented, in ascending order, by the genera *Nicrosaurus*, *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus*.

Majority rule consensus tree from the analysis with 14 ordered multistate characters (Fig. 5.4): The ordering of 14 multistate characters resulted in numerous topological differences to the MPTs based on the analysis with unordered character states: (1) Non-phytosaurid phytosaurs are not resolved, and the high number of MPTs results largely from variations in the topology within this group. Three trends may be seen in this trees: in 89% of the MPTs, *Paleorhinus sawini* and *Mesorhinosuchus fraasi* are placed at the base of Phytosauria. 80% of the trees show *Paleorhinus bransoni*, *Paleorhinus*

scurriensis, and *Paleorhinus magnoculus* as the most derived non-phytosaurid phytosaurs. *Ebrachosuchus neukami* and *Francosuchus angustifrons* form a separate clade. (2) *Rutiodon carolinensis* is consistently nested deeply within non-angistorhinine Phytosauridae rather than at the base of Phytosauridae. (3) This analysis found the same clade of most derived Phytosauridae, however, *Pseudopalatus* and *Arribasuchus* form consistently a monophyletic clade rather than the successive outgroups to *Mystriosuchus*.

Strict consensus tree of three selected optimal MPTs (Fig. 5.5): The non-phytosaurid phytosaurs are almost fully resolved. *Paleorhinus sawini* and *Mesorhinosuchus fraasi* represent the most basal taxa, followed by *Ebrachosuchus neukami* + *Francosuchus angustifrons*, *Promystriosuchus ehlersi*, and "*Parasuchus hislopi*". The previously recognised clade composed of *Paleorhinus magnoculus* and *Paleorhinus bransoni* + *Paleorhinus scurriensis* forms the sistergroup of Phytosauridae. Within Phytosauridae, Angistorhininae are resolved into a *Brachysuchus megalodon*, which forms the sistergroup of *Angistorhinus grandis* + *Angistorhinus talainti*. A clade *Leptosuchus crosbiensis* + *Smilosuchus gregorii*, already found in the majority of trees of the previous analysis, forms the base of non-angistorhinine Phytosauridae. *Rutiodon carolinensis* is more derived, and placed in a the sistergroup-relation with *Leptosuchus adamanensis*. The clade *Nicrosaurus* , *Arribasuchus* + *Pseudopalatus*, and *Mystriosuchus* is present as the most derived Phytosauridae.

5.4.3 Discussion and evaluation of the results

5.4.3.1 The status of *Paleorhinus*

For a long time, the primitive phytosaurs characterised by more anteriorly placed external nasal openings in combination with the parieto-squamosal bar at level of the skull roof were regarded as the stem-group of the more advanced phytosaur taxa. The idea that certain species were ancestral or closer related to different lineages among phytosaurs contributed to the acceptance of several generic (in later works lowered to subgeneric rank) names (CAMP 1930; GREGORY 1962a, 1969; WESTPHAL 1976; CHATTERJEE 1978). More recent reviewers tried to establish the monophyletic status of this assemblage of primitive forms, and grouped them either under the oldest valid genus group name, *Paleorhinus* (BALLEW 1989; HUNT & LUCAS 1991; HUNT 1994), or included more than one genus within a clade Paleorhininae (LONG & MURRY 1995).

LONG & MURRY (1995: 35) listed numerous diagnostic features of Paleorhininae: nares anterior to antorbital opening; posterior border of supratemporal fenestra at level with skull roof; posterior process of squamosal small; postnarial portion of skull long; interpterygoid vacuity long; postorbito-squamosal bar narrow; skull roof not strongly sculptured. However, these are symplesiomorphies for Phytosauria. Two more characters quoted are vague and of dubious value: the orbits being directed dorsally or dorsolaterally, and the quadrate being defined as low. Among the four autapomorphies suggested by BALLEW (1989: 317), characters 5 and 6 are variable not only within non-phytosaurid phytosaurs, but also within more derived phytosaurs: the nares are not consistently directed anteriorly, as exemplified by the dorsal orientation in *Promystriosuchus ehlersi* and *Paleorhinus magnoculus* (CASE 1922; DUTUIT 1977b), and the orbits do not face dorsally in "*Parasuchus hislopi*" (CHATTERJEE 1978) and *Paleorhinus sawini* (LONG & MURRY 1995). Her character 7 "posterior border of naris in front of anterior border of antorbital fenestra" represents an intermediate state of a multistate character transformation (here character 10[1]) and is a synapomorphy of a more inclusive group, the Phytosauria. Regarding the last postulated synapomorphy of *Paleorhinus*, "posttemporal fenestra laterally expanded above the oar-shaped process of the opisthotic and narrowly compressed", the validity is dubious. According to published reconstructions, I do not see much difference to other taxa because posttemporal fenestrae that are of similar shape and size occur in other, more derived phytosaurs as well. Lastly, the large quadrate foramen cited by HUNT & LUCAS (1991) in favour for *Paleorhinus* holds not true for all taxa incorporated by them in that genus (see character 40) and is similarly developed in *Mystriosuchus*, and thus not *a priori* diagnostic for *Paleorhinus*. In conclusions, all previous studies failed to identify unequivocally autapomorphic characters supporting a monophyletic clade that comprises all basal phytosaur taxa.

Regardless of the settings, the analyses performed in this study do not support an monophyletic group comprising all non-phytosaurid phytosaurs, but suggests that "*Paleorhinus*" or Paleorhininae, respectively, is a grade of generally primitive taxa that forms the paraphyletic stem-group of Phytosauridae. While the clade Phytosauridae is a robust terminal component of all MPTs obtained, the incongruences among the trees as expressed in the consensus (Fig. 5.4) are largely caused by topological instability within the basal phytosaur taxa.

Based on the data matrix presented in Appendix A, the most parsimonious MPTs that include a monophyletic "*Paleorhinus*" show a length of 209 steps, i. e. 6 steps more than the MPTs without this constraint (Tab. 5.1). A clade "*Paleorhinus*" is supported by only two derived characters that show no homoplasies on all 60 trees found to be most

parsimonious under this constraint: character 8, the septomaxilla is extended posteriorly, and character 26, the dorsal surface of the squamosal shows a depression or a groove. These characters exclusively shared by basal phytosaurs are by far outnumbered by the numerous synapomorphies that various subsets of non-phytosaurid phytosaurs have in common with Phytosauridae. It is therefore concluded that the monophyletic status of a group including all non-phytosaurid phytosaurs is unsupported by parsimony, and neither the genus *Paleorhinus* in the meaning of BALLEW (1989), HUNT & LUCAS (1991) and LONG & MURRY (1995) nor Paleorhininae are accepted in this study.

The most robust clade among non-phytosaurid phytosaurs is represented by *Ebrachosuchus neukami* and *Francosuchus angustifrons* (Fig. 5.5, node C), which is the only clade that is also reproduced in the bootstrap analysis (Fig. 5.7). This clade is well supported by character 11, the presence of an infranasal recess (paralleled in *Nicrosaurus*). Both taxa are also characterised by a reversal, the only phytosaurs having lost the overhang of the parietals over the supraoccipital shelf (character 24, state 0). The identification of this clade in the parsimony analysis coincides with the suggestion of a number of authors that *Francosuchus* and *Ebrachosuchus* are actually conspecific (GREGORY 1962a; WESTPHAL 1976; CHATTERJEE 1978; HUNT & LUCAS 1991; LONG & MURRY 1995), although the postulated synonymy appears to have been based more on the contemporaneous occurrence at the same locality rather than on morphological grounds. However, it should be noted that both taxa are dissimilar in the characters 22, 31, and 32, and grossly at variance regarding character 6, the number of teeth and character 20, the width of the postorbito-squamosal bar. Among Phytosauridae, the same authors accepted even a generic segregation of specimens on the basis of identical character differences. Such discrepancies in the character state distribution and their assessments underline the need for a taxonomic review of the European basal phytosaurs.

Another clade consisting of *Paleorhinus bransoni* and *Paleorhinus scurriensis* in sistergroup relationship with *Paleorhinus magnoculus* occurs frequently among the MPTs (Fig. 5.5, node G). This clade is mainly supported by a unique character state for basal phytosaurs, a high jugal (18[2]), and by two reversals resulting in a long prefrontal (13) and the quadrate foramen being not visible in lateral view (41). However, all these character states are unknown for *Paleorhinus scurriensis*, and the status of *Paleorhinus magnoculus* is doubtful (see subsection 5.2.1). Thus, the existence of this clade must be regarded as weakly supported by shared derived characters, although it is arguable that all three taxa are closer related to Phytosauridae than to any other basal phytosaur (see below). By contrast, the sistergroup relationship between *Paleorhinus bransoni* and *Paleorhinus scurriensis* is more firmly based on character 45, the palatines being visible

on the palatal vault, which is otherwise only paralleled among non-angistorhinine Phytosauridae (*Nicrosaurus*; *Leptosuchus crosbiensis*). Pending a restudy of the type specimens, the close relationship advocated here suggests a generic, and perhaps even specific, identity.

The cladogram resulting from *a posteriori* down-weighting of less homoplastic characters (Fig. 5.5) suggests that the non-phytosaurid phytosaurs and Phytosauridae form a set of internested subclades, which include a successively smaller number of primitive phytosaur taxa. The result of the bootstrap analysis (Fig. 5.7) as well as the highly variable interrelationships of basal phytosaurs on all MTPs indicate that such clades are far from being robust components of the cladogram. For this reason, all subclades that involve non-phytosaurid phytosaurs and Phytosauridae are identified only tentatively, and no definite conclusions regarding taxonomy and nomenclature are drawn.

In the cladogram (Fig. 5.5), *Paleorhinus sawini* and *Mesorhinosuchus fraasi* are indicated as most primitive phytosaurs below node B. This assessment is based on the absence of the derived states of characters 13 (reduced length of the prefrontal), 19 (jugal-quadratojugal complex), and 41 (quadrate foramen visible both laterally and posteriorly). However, characters 13 and 41 are subsequently reversed in a clade of more derived non-phytosaurid phytosaurs (see above). More importantly, on closer inspection it is found that, regarding each character, the state is actually unknown in at least one of the taxa. This, in combination with the presence of the similar plesiomorphic states in closely related forms, suggests that the basal position of *Paleorhinus sawini* and *Mesorhinosuchus fraasi* could well be the result of missing data rather than the actual absence of derived character states.

The phytosaurs in the cladogram positioned above *Ebrachosuchus* + *Francosuchus* (node D) share two derived characters: 40, the size of the quadrate foramen is reduced (reversed in *Paleorhinus magnoculus* and *Mystriosuchus*), and 44[3], the palatine is elongated and extends beyond the choana. Character 44 is less reliable, showing multiple reversals within the ingroup.

A clade including "*Parasuchus hislopi*", *Paleorhinus magnoculus*, *Paleorhinus bransoni*, *Paleorhinus scurriensis*, and Phytosauridae (node E) seems to be the best supported monophylum that includes basal and more derived phytosaurs. The clade is defined by the ventral extension of the paroccipital process of the squamosal (character 36). The plesiomorphic state is clearly absent in the more basal phytosaurs (except *Mesorhinosuchus*, in which the character state is unknown), and among the ingroup taxa it is reversed only once in *Paleorhinus magnoculus*. A second synapomorphy might be represented by the reduction of the interpterygoid vacuity to a small posteriorly positioned

opening (48[2]), albeit this character proves to be highly homoplastic among Phytosauridae and shows multiple reversals to a longer, slit-like outline.
The squamosal overhanging the quadrate (character 31) suggests that *Paleorhinus magnoculus*, *Paleorhinus bransoni*, and *Paleorhinus scurriensis* are more closely related with Phytosauridae (node F) than with any other non-phytosaurid phytosaur. The character is, however, independently acquired by *Francosuchus angustifrons*, and subsequently reversed in *Brachysuchus megalodon* and *Mystriosuchus* among Phytosauridae.

5.4.3.2 The phylogenetic position of *Mystriosuchus*

The relationships of *Mystriosuchus*

Both the conflicting most recent hypotheses regarding the relationships of *Mystriosuchus* have been outlined above (Figs. 5.1, 5.2). As BALLEW's view essentially corresponds to the result of this analysis, which is treated in more detail below, I will briefly discuss here only the evidence presented so far for the competing hypothesis.

LONG & MURRY (1995: 34) quote a number of characters shared by Mystriosuchidae (*Mystriosuchus* and primitive phytosaurs grouped as Paleorhininae): squamosal diminutive, compressed dorsoventrally and truncated posteriorly; well defined lateral ridge of the squamosal; posttemporal fenestra always very small; rostrum slender, lacking a crest; external nares face anteriorly; homodont dentition (except perhaps in *Paleorhinus sawini*). LONG & MURRY also emphasise that the nares of *Mystriosuchus* is depressed below the skull roof, as opposed to *Arribasuchus* and *Pseudopalatus*. This, and the primitive state of the squamosal, has also been suggested by HUNT & LUCAS (1989b: 343) in favour of *Mystriosuchus* being "more closely related to *Paleorhinus* [...] or *Rutiodon*", but with the apt restriction "pending phylogenetic analysis". Unfortunately, neither LONG & MURRY nor HUNT & LUCAS did present a discussion of their views of the affinities of *Mystriosuchus*. I have several reservations regarding the characters quoted. Firstly, with the exception of the lateral ridge of the squamosal, these characters must be considered plesiomorphic on the level of Phytosauria. Secondly, most of the definitions are vague, and some do not apply. The nares of primitive phytosaurs open anterodorsally at best, and the definition does not describe the nares of *Mystriosuchus* properly (see part 3.3.2.1). The posttemporal fenestra is not particularly small in primitive phytosaurs (e.g. BALLEW 1989; part 5.4.3.1). There are also difficulties with the absence of a posterior process of the squamosal and the term homodont, both as defined in this study (subsection 5.3.2: characters 5, 30, 31). Problems related to the

elevation of the nares are discussed in part 2.3.4.1 (3). In conclusion, the hypothesis of a close relationship of *Mystriosuchus* with primitive phytosaurs seems to rest basically on similarities that must be considered symplesiomorphies. The only unequivocal synapomorphy supporting such a clade is the presence of a marked lateral ridge of the squamosal.

A third hypothesis was suggested earlier by GREGORY (1962a, 1969) and CHATTERJEE (1978), who concluded that *Mystriosuchus* is more closely related to the European non-phytosaurid phytosaurs (here represented by *Francosuchus* and *Ebrachosuchus*) than to any other phytosaur taxon. Aside from plesiomorphic character states common to all primitive phytosaurs and *Mystriosuchus*, the significance of which has been doubted above, both authors put much stress on the similar, strongly elongated snout of *Ebrachosuchus neukami* and *Mystriosuchus planirostris*. However, *Promystriosuchus ehlersi* shows a comparable snout length, and following the referral of "*Belodon plieningeri*" GPIT 261/001 to *Mystriosuchus*, a very long snout is not necessarily a derived character of the genus.

The most significant phylogenetic conclusion of this study is that *Mystriosuchus*, the arguably most derived phytosaur taxon in respect to a number of characters, is not closely related to non-phytosaurid phytosaurs or any taxon included in the stem-group of Phytosauridae. Regardless whether ordered or unordered multistate characters have been employed, the parsimony analyses resulted in MPTs consistently showing a terminal clade that comprises both *Mystriosuchus* species in a sistergroup relationship to *Arribasuchus* + *Pseudopalatus* (Figs. 5.3 - 5.5). This configuration is also supported by the bootstrap analysis (Fig. 5.7). To put the stability of this clade on a more rigorous test, the data matrix with ordered multistate characters was re-run through PAUP enforcing a variety of constraints on the tree topology. The results are presented in Table 5.1.

The shortest trees that include a monophylum of *Mystriosuchus* and any non-phytosaurid phytosaur (represented by *Promystriosuchus ehlersi*) are seven steps longer than the MPTs found in the analysis without topological constraints. It needs four additional, i.e. a total of 11, steps for a clade of *Mystriosuchus* with a primitive European phytosaur taxon (*Ebrachosuchus neukami*), which corresponds to the hypothesis suggested by GREGORY (1969) and CHATTERJEE (1978), to appear among the most parsimonious trees. A total of 14 additional evolutionary transformations are required to arrive at the hypothesis suggested by LONG & MURRY (1995) and HUNT & LUCAS (1989b) that *Mystriosuchus* is the sistergroup of all primitive, non-phytosaurid phytosaurs.

Table 5.1: Changes in length of the most parsimonious trees under various constraints.

constraint	number of MPTs	tree length (steps)	remarks
monophyletic *Paleorhinus sensu* BALLEW (1989) = Paleorhininae *sensu* LONG & MURRY (1995)	60	209 (+6)	no changes in the topology of the remaining Phytosauridae; constraint clade is unresolved except *Ebrachosuchus* + *Francosuchus*
monophyletic *Mystriosuchus* + non-phytosaurid phytosaurs	7	217 (+14)	no changes in the topology of the remaining Phytosauridae;
monophyletic *Mystriosuchus* + *Promystriosuchus ehlersi*	77	210 (+7)	constraint clade forms a sistergroup with the remaining Phytosauridae
monophyletic *Mystriosuchus* + "*Parasuchus hislopi*"	18	213 (+10)	*Promystriosuchus ehlersi* and constraint clade are successive outgroup to the remaining Phytosauridae
monophyletic *Mystriosuchus* + *Ebrachosuchus neukami*	2	214 (+11)	constraint clade is nested within paraphyletic non-phytosaurid phytosaurs
monophyletic *Leptosuchus*	56	205 (+2)	Phytosauridae are unresolved
monophyletic *Leptosuchus crosbiensis* + *Leptosuchus adamanensis* + *Smilosuchus*	16	203 (-)	included among the initial 35 MPTs
monophyletic Rutiodontidae *sensu* LONG & MURRY (1995)	44	207 (+4)	*Mystriosuchus* is the sistergroup of the constraint clade
monophyletic "*Rutiodon*" *sensu* BALLEW (1986) = Rutiodontinae LONG & MURRY (1995)	14	203 (-)	included among the initial 35 MPTs

In conclusion, the phylogenetic hypothesis that *Mystriosuchus* is nested among Phytosauridae as the most derived clade is much more parsimonious and robuster than any previous phylogenetic hypothesis of this taxon. Therefore, the reconstruction of the relationships of the four most derived phytosaur taxa as shown in Figure 5.5 is assessed here the most likely to reflect the actual phylogenetic history of *Mystriosuchus*. The suggestion of a clade *Mystriosuchus* + *Paleorhinus*/Paleorhininae advocated most recently by LONG & MURRY (1995) is so much less supported by my data that it can be virtually rejected as a alternative worth further consideration. It would even be more parsimonious to assume a closest relationship of *Mystriosuchus* with any other taxon of basal phytosaurs.

The clade *Mystriosuchus* + (*Pseudopalatus* + *Arribasuchus*) is supported by four synapomorphies that are retained in all species and can be securely identified as autapomorphies, because the derived character states are not developed in closely related phytosaur taxa. These include the derived states of

character (6[2]): number of teeth increased to more than 47, which is a unique feature among non-angistorhinine phytosaurids, but has been convergently acquired by *Ebrachosuchus neukami*, *Promystriosuchus ehlersi*, and *Angistorhinus grandis*.

character (23): rounded top of the parietal-supraoccipital complex, which in this clade is combined with ventrally directed squamosal processes of the parietals.

character (24[2]): a horizontal ledge of the parietals is developed and overhangs the supraoccipital shelf (paralleled in angistorhinine phytosaurs).

character (33[3]): the parieto-squamosal bar is depressed below the skull roof for more than 25% of the skull height, and includes the most extreme values found among phytosaurs.

Two more characters are identified in support of the monophyly of (*Mystriosuchus* and *Arribasuchus* + *Pseudopalatus*), however, both are homoplastic among closely related taxa of non-angistorhinine phytosaurids. The snout is long (1[2]), as in *Nicrosaurus* species B and *Rutiodon carolinensis*, and the suborbital fenestra is strongly reduced (47[2]; paralleled in *Leptosuchus crosbiensis* and *Smilosuchus gregorii*).

By contrast, BALLEW (1989) found that *Mystriosuchus planirostris* is most closely related to *Pseudopalatus pristinus* (Fig. 5.1), and tentatively included both taxa as subgenera within one genus, which she incorrectly named *Pseudopalatus*. One might suspect that BALLEW's different configuration of the most derived phytosaur taxa roots in the fact that her data did not include *Mystriosuchus* species B. However, a re-run of my data matrix, with *Mystriosuchus* species B excluded, came up with an identical topology of *Mystriosuchus planirostris* as in Figure 5.4, suggesting that BALLEW's different interpretation is not the result of missing data, but is based on the different nature of the data matrices employed. A second re-run with the constraint of a monophyletic clade (*Mystriosuchus planirostris*, *Mystriosuchus* species B, *Pseudopalatus pristinus*) resulted in one MPT with the insignificantly greater length of 204 steps compared to the initial analysis. Judged by the criterion of tree length, BALLEW's phylogenetic interpretation is a reasonable alternative that cannot be easily dismissed.

However, the quality of the shared characters of *Mystriosuchus* + *Pseudopalatus pristinus* as determined in this analysis is rather weak. Only character 4 (concave lateral rim of the maxilla), corresponding to the triangular skull outline in dorsal view of BALLEW (1989), is unequivocal. The other potential synapomorphies are homoplastic within Phytosauridae: long snout (1[2]: also *Rutiodon carolinensis*, *Nicrosaurus* species B, polymorph in *Angistorhinus buceros*), bipartite dentition ("homodont" in BALLEW; reversal to 5[1]: also *Rutiodon carolinensis*, *Nicrosaurus* species B; state is unknown in *Mystriosuchus* species B), and slender jugal (reversal to 18[0]: also *Nicrosaurus* species B). Two synapomorphies postulated by BALLEW (1989: 332) are plesiomorphic (uncrested rostrum) or present in *Arribasuchus* as well (nasals surround the nares in cone-like fashion). By contrast, the clade *Arribasuchus buceros* + *Pseudopalatus*

pristinus is unequivocally supported by the derived characters (9), nares elevated above skull roof, although this character must be considered problematical (part 2.3.4.1 (3)), (15[1]), high pre-infratemporal shelf, (28[3]), strongly developed medial lamella of the squamosal, and both taxa additionally share (30[3]), very long posterior process of the squamosal, which is otherwise only developed in *Leptosuchus crosbiensis*. This suggests that a clade *Mystriosuchus* + (*Pseudopalatus* + *Arribasuchus*)) is the more plausible hypothesis.

Conclusions regarding the diagnostic characters of *Mystriosuchus*

Nine diagnostic characters of *Mystriosuchus* have been determined by their exclusiveness and are further discussed in part 3.1.2.1. Based on the phylogenetic analysis, two more characters states turned out to represent characters that have been modified from the condition reconstructed for a hypothetical ancestor, although in both cases the similar states occur in other phytosaur taxa as well. The cladogram, however, shows these taxa as only distantly related with *Mystriosuchus*. The probability of these characters being non-homoplastic is slim, and they may be added to the list of diagnostic characters for *Mystriosuchus*:

character (27): the squamosal shows a sharp lateral ridge dividing the horizontal from the vertical plane. According to the character state tree, the same condition was acquired by the hypothetical ancestor of Phytosauria, and subsequently lost in the lineage leading to Phytosauridae. The derived character state secondarily appears again also in *Angistorhinus talainti* and *Rutiodon carolinensis*.

reversals of characters (30) and (31): the posterior process of the squamosal is strongly reduced to a length of less than 10 mm (30[1]), and the process disappears altogether in *Mystriosuchus planirostris*. Probably as a corollary effect of the same process, the quadrate forms the posteriormost point of the skull (31).

The analysis identified two additional traits as diagnostic for *Mystriosuchus*: the lateral rim of the maxilla is concave (character 4) and a reversal of the height of the jugal to the plesiomorphic slender condition (character 18). However, the same character states must be interpreted as convergently acquired by *Pseudopalatus pristinus*, and as long as it is not fully established that *Pseudopalatus* is the sistergroup of *Arribasuchus*, I do not propose these characters as autapomorphies of *Mystriosuchus*.

The result of the phylogenetic analysis outlined here, however preliminary, allows to identify these derived character traits which evolved only once within phytosaurs, and therefore represent synapomorphies that define higher categories. In accepting the hypothesis of a clade *Mystriosuchus* + non-phytosaurid phytosaurs, the same characters have previously been interpreted as homoplastic, and were therefore necessarily estimated as having limited or no significance for phylogenetic reconstructions (HUNT & LUCAS 1989b; LONG & MURRY 1995). The identification is independent from the question whether *Mystriosuchus* is closer related to *Pseudopalatus*, or to a clade comprising *Pseudopalatus* + *Arribasuchus*. Basically, the main phylogenetic and developmental conclusions drawn by BALLEW (1989) are confirmed, although my interpretation rests on a refined and expanded data base.

(1) In all phytosaurs, the external nasal openings are shifted backwards from the tip of the premaxillae (10[1]). A non-terminal position, but still in front of the antorbital fenestrae, represents an intermediate state seen in non-phytosaurid phytosaurs. The nares achieves independently a more progressive state in reaching the level of the antorbital opening (10[2]) in two lineages, *Mesorhinosuchus fraasi* and *Promystriosuchus ehlersi*. The most extreme position is represented in a third lineage, in which the nares are placed above the antorbital fenestrae and may be located just in front of the orbits (10[3]). This state is a synapomorphy of all Phytosauridae.

(2) The expansion of the lateral part of the paroccipital process of the opisthotic in dorsoventral direction (39) represents another autapomorphy of Phytosauridae.

(3) The depression of the parieto-squamosal bar significantly below the level of the skull deck (33[2]) is a true synapomorphy of the most derived phytosaurs *Leptosuchus*, *Smilosuchus*, *Rutiodon*, *Nicrosaurus*, *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus*. These taxa that have been informally characterised as "advanced phytosaurs" or "*Nicrosaurus*-grade" thus form a clade, and not an evolutionary grade as probably intended by the introduction of such terms. The recession of the postorbito-squamosal bar continues further (33[3]) in the clade Pseudopalatinae formed by *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus*, and finds its maximal expression in the latter genus. The distribution suggests a linear and non-reversed trait. However, provided the condition of *Paleorhinus scurriensis* can be confirmed, there is evidence that the beginnings of the same trait developed a second time among primitive phytosaurs independently from the lineage to Phytosauridae.

(4) The rounded parietal-supraoccipital complex (23) within phytosaurs defines a clade comprising *Arribasuchus*, *Pseudopalatus*, and *Mystriosuchus*. This character state is coupled with steeply ventrolaterally to vertically directed squamosal processes of the

parietals. Since the latter is almost certainly a structural necessity for achieving an increased depression of the parieto-squamosal bar (state 33[3]), the rounded top of the parieto-squamosal complex may be an indicator for the presence of such a highly derived state of the supratemporal fenestra in *Angistorhinopsis ruetimeyeri* (HUENE 1922).

The following features are interpreted as homoplastic character states which either evolved independently in *Mystriosuchus* or represent reversals. It is remarkable that the homoplastic characters (1) and (2) are not restricted to the lineage of non-angistorhinine phytosaurs, but the same processes must have taken place a second time within angistorhinine phytosaurs.

(1) Although the abbreviated length of the squamosal of *Mystriosuchus* and non-phytosaurid phytosaurs may be similar at first glance, this character state cannot not prove a close relationship. The analysis strongly suggests that the elongation of the posterior process of squamosal, an autapomorphy of Phytosauridae that represents a unique feature of phytosaurs among Archosauria, has been reversed in *Mystriosuchus*. This is further corroborated, firstly, by the observation that the reduction of the squamosal length in *Mystriosuchus* is not uniform: *Mystriosuchus planirostris* still shows a short posterior process, whereas in *Mystriosuchus* species B the posterior tip of the squamosal has even receded in front of the posterior rim of the quadrate, the most primitive condition. Since in non-phytosaurid phytosaurs the presence, and the length of the posterior process in respect to the quadrate, is similarly at variance, both characters states must be to some degree homoplastic even under the assumption of sistergroup relationship of *Mystriosuchus* and all basal phytosaurs. The character state as expressed in *Mystriosuchus* is thus indeed a very derived condition (BALLEW 1989). Secondly, the analysis also suggests that the same reduction took place independently within Angistorhininae, as exemplified by *Brachysuchus*. The functional significance of presence or absence of a posterior process still lacks a convincing explanation, and represents an area of future research.

(2) The large to fully developed medial extension of the squamosal, which is a characteristic of *Nicrosaurus*, *Pseudopalatus* and *Arribasuchus*, is reduced in *Mystriosuchus* to an incipiently narrow lamella. The reduction results primarily in a secondary re-opening of the supratemporal fenestra, which is, in respect to the width of the opening, comparable to a character state seen in *Leptosuchus crosbiensis* and *Smilosuchus*. The variable nature of the closing lamella is furthermore supported by the observation that a probably similar lamella was independently developed in *Angistorhinus talainti*, leading to a crescent-shaped, narrow supratemporal fenestra in this species. The

functional implications of the reversal are unknown, and any further interpretation is speculative. It is, however, interesting to note that among the Phytosauridae with depressed parieto-squamosal bars large supratemporal fenestrae are correlated alternatively with two other features of the temporal region. The reduction of the absolute width of the postorbito-squamosal bar could suggest that the thickening of this structure in *Mystriosuchus* is a corollary phenomenon for statical reason, and represents indeed an autapomorphy unique to that genus. The greatly enlarged vertical surface of the squamosal in *Leptosuchus crosbiensis* and *Smilosuchus gregorii*, which both lack a medial extension of the postorbito-squamosal bar, might have served for a similar purpose.

(3) The lateral ridge on the squamosal in *Mystriosuchus* is a homoplastic character, having risen independently from non-phytosaurid phytosaurs. This is not only a consequence of the topology of *Mystriosuchus* in the MPTs, but also indicated by the presence of a similar, if less well developed structure in some specimens of *Rutiodon carolinensis*, and *Angistorhinus talainti*. The squamosal ridge represents the only derived structure that has been quoted in support for a close relationship of *Mystriosuchus* and non-phytosaurid phytosaurs.

(4) The large size of the quadrate foramen in both *Mystriosuchus* species is not a synapomorphy with primitive phytosaurs, but represents a reversed condition that evolved from the reduced size of the foramen in less derived Phytosauridae. This is supported by the observation that the quadrate foramen of *Mystriosuchus* developed into an even larger size than seen in any other phytosaur.

5.4.3.3 Conclusions regarding the status of higher categories

Establishing the phylogenetic position of *Mystriosuchus* within Phytosauridae has important corollary effects on the systematic and nomenclature of higher categories among phytosaurs. My concept of the synonymy of higher categories follows QUEIROZ & GAUTHIER (1990) in regarding suprageneric names and clades synonymous when they refer to the same common ancestor, as defined by the taxa originally included in comparison with the position in the cladogram Figure 5.5. This means that both the original restriction in terms of inclusiveness and the (usually character-based) definition are largely disregarded.

In their recently published review, LONG & MURRY (1995) established the most elaborated framework of higher taxa within Phytosauria so far (Fig. 5.2), which includes all names of family rank erected previously. Their concept of Mystriosuchidae and Paleorhininae becomes paraphylletic, and is unacceptable in their intended composition; in

a phylogenetic definition ("the last common ancestor of non-phytosaurid phytosaurs, either with or without *Mystriosuchus*, and all of its descendants"), both names are synonymous with Phytosauria. Mystriosuchinae is identical to *Mystriosuchus*, and therefore at present redundant, but might be applicable in the future when taxa are found to branch off between node O and *Mystriosuchus*. The existence of a clade Rutiodontinae (in its original inclusiveness, *Rutiodon*, *Leptosuchus* and *Smilosuchus*) is not substantiated with confidence, and must be left open. Angistorhininae and Pseudopalatinae are still in existence, however, the latter is more inclusive (plus *Mystriosuchus*) and both are in need of redefinition. Both taxa have been originally defined entirely on diagnostic characters (character-based and apomorphy-based taxon definitions), and such taxa are thus highly sensible to changes in the ideas which subordinate taxa are to be included (QUEIROZ & GAUTHIER 1990). Phytosauridae, redefined by DOYLE & SUES (1995), does not change in composition.

All preexisting suprageneric category names (except Phytosauridae) are redefined here phylogenetically to achieve a stable scheme, regardless of changes in their inclusiveness in the future, and a diagnosis of each taxon is given based on the results of this parsimony analysis. I do not define clades which are, in my opinion, still weakly supported (nodes B, D, E, F, J, and L in Fig. 5.5) and which might prove unstable when new or refined data is incorporated. Likewise, I refrain from proposing any nomenclatural changes at generic or species level (nodes C, K, and M). Although problems in the composition and diagnosis of some genera are pointed out, this should await a more detailed revision of the comprising taxa.

In all phylogenetic studies of phytosaurs as well as archosaurs in the past 20 years, Phytosauria (or the synonym Parasuchia) is given ordinal rank, while the next most inclusive taxon, Phytosauridae, has been redefined as family-group name (DOYLE & SUES 1995). It is a well-known fact, that the strictly dichotomous classification scheme constructed from a cladistic analysis may be not fully compatible with the traditional Linnean classification. Some problems arose as a result of this study: although the phylogeny presented here is logically consistent with previous classifications (WILEY *et al.* 1991), suprageneric existing taxa of similar rank do not match the hierarchical structure, i. e. the level of inclusiveness (e.g. the subfamilies Angistorhininae and Pseudopalatinae), and there are not sufficient categorial ranks available to reflect the hierarchy of definable nodes. Possible solutions, apart from abandoning Linnean classification altogether in favour of a numerical system or indenting taxa in print, could be to upgrade old (e.g. Phytosauridae), and create new, names above the family-group level reglemented by the ICZN, or to insert a plethora of uncommon intermediate ranks (e.g. tribus, subtribus). The best solution might be to follow the recommendations of

WILEY *et al.* (1991) to place less inclusive taxa than Phytosauridae at same rank and to sequence in their order of branching. However, bearing in mind the preliminary state of the analysis, no new suprageneric taxa are formally erected, and new clades are refered to in open nomenclature derived from the alphabetical indication of the node used in the cladogram.

Clade A: Phytosauria JAEGER, 1826

Synonyms: Parasuchia LYDEKKER, 1888; Parasuchidae LYDEKKER, 1888.
Definition: Phytosauridae, and all taxa sharing a more recent common ancestor with them than with Crocodylia.
Discussion: Maintaining the inclusiveness of Phytosauria, as intended by the initially node-based definition of Phytosauria " *Paleorhinus*, Phytosauridae, and all descendants of their closest common ancestor" (DOYLE & SUES 1995: 546), necessitates that all taxa included in non-phytosaurid phytosaurs are referred to, or placed in synonymy with, the genus *Paleorhinus*. This study suggests, however, that *Paleorhinus* (*sensu* BALLEW 1989 and HUNT & LUCAS 1991) is a paraphyletic group. The original definition thus tied to the type species *Paleorhinus bransoni* would result in the exclusion of a number of taxa that are universally regarded as phytosaurs. Hence, Phytosauria is redefined here using a stem-based definition, in order to allow the inclusion of any taxon that may come forward in future reviews of the systematics of basal phytosaurs.
Generic composition: *Ebrachosuchus* KUHN, 1936, *Francosuchus* KUHN, 1933, *Mesorhinosuchus* KUHN, 1961, *Paleorhinus* WILLISTON, 1904, "*Parasuchus*" LYDEKKER, 1885, *Promystriosuchus* CASE, 1922, as defined in subsection 5.2.1, and all Phytosauridae.
Diagnostic (synapomorphic) characters:
see characters listed under (1) to (16) in part 5.3.1.1.

Clade H: Phytosauridae JAEGER, 1826

Synonyms: Rutiodontidae LONG et MURRY, 1995; BALLEW (1989): unnamed clade, figure 1, node C.
Definition: the last common ancestor of *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, "*Pseudopalatus*", "*Rutiodon*", and all descendants of their closest common ancestor (DOYLE & SUES 1995: 546).
Referred genera: *Brachysuchus* CASE, 1929, *Angistorhinus* MEHL, 1913, *Leptosuchus* CASE, 1922, *Smilosuchus* LONG et MURRY, 1995, *Rutiodon* EMMONS, 1856,

Nicrosaurus O. FRAAS, 1866, *Arribasuchus* LONG et MURRY, 1995, *Pseudopalatus* MEHL, 1928, and *Mystriosuchus* E. FRAAS, 1896, as defined in subsection 5.2.1.

Discussion: The diagnosis of Phytosauridae in BALLEW (1989) and LONG & MURRY (1995: 38) correctly include characters corresponding to (10[3]) and (30[2]). LONG & MURRY also identify character (27) as diagnostic, although it must be regarded as inherited plesiomorphic feature according their classification. By contrast, the presence of a "hook-like process" (BALLEW: character 10, here paroccipital process of the squamosal) characterises a more inclusive clade (node E), and I do not accept her character 11, nares opening dorsally, for reasons stated above. LONG & MURRY's other diagnosing features (squamosal rounded or pointed terminally [sic!]; rostrum usually deep; strong tendency towards heterodonty) are both too vague and variable among the taxa to be of any diagnostic value.

Diagnostic (synapomorphic) characters:

character (10[3]): the posterior rim of the nares is positioned above and posterior to the anterior rim of the antorbital fenestra.

character (26): the groove on the dorsal surface of the squamosal is lost (reversal).

character (39): the lateral extremity of the paroccipital process of the opisthotic is dorsolaterally enlarged.

The following, mostly derived character states are not unequivocally distributed, but at present accepted as additional synapomorphies of Phytosauridae:

character (8): the posterior extent of the septomaxillary is reduced, terminating in front of the posterior rim of the nares. This character is only tentatively identified as synapomorphic, because the posterior border of the septomaxilla is unknown in *Paleorhinus bransoni*, *Paleorhinus sawini*, *Mesorhinosuchus fraasi*, and *Promystriosuchus ehlersi*, and (8) may potentially characterise a more inclusive group.

character (16[2]): the infratemporal fenestra extends forward below the anterior half of the orbit. The same character state is independently acquired in *Ebrachosuchus*, and the condition is reversed to (16[1]) in *Rutiodon carolinensis*.

character (27): the lateral ridge of the squamosal is lost (reversal). However, the phytosaurid taxa *Angistorhinus talainti*, *Rutiodon carolinensis*, and *Mystriosuchus* redevelop, each independently, the apomorphic state.

character (30[2]): the posterior process of the squamosal exceeds a length of 10 mm. The process is reduced in *Brachysuchus megalodon* and *Mystriosuchus*.

Clade I: Angistorhininae CAMP, 1930

Definition: *Brachysuchus megalodon*, *Angistorhinus grandis*, and *Angistorhinus talainti*, and all taxa that are more closely related with them than with any other member of Phytosauridae.

Referred taxa: *Brachysuchus megalodon* CASE, 1929, *Angistorhinus grandis* MEHL, 1913, and *Angistorhinus talainti* DUTUIT, 1977, as defined in subsection 5.2.1. Taxa that are not considered in the analysis but most likely pertain to this clade include *Angistorhinus alticephalus* STOVALL et WHARTON, 1936, *Angistorhinus aeolamnis* EATON, 1965, and *Angistorhinus maximus* MEHL, 1928.

Discussion: BALLEW (1989: 318) diagnosed *Angistorhinus* (in the composition of Angistorhininae here) by, firstly, "a completely dorsal supratemporal fenestra coupled with external nares that have posterior borders superior and posterior to the anterior border of the antorbital fenestra". This combination of a plesiomorphic and apomorphic character for a more inclusive ingroup does not constitute a synapomorphy. The second autapomorphy identified are long cojoined parietals, corresponding to my character (21). LONG & MURRY (1995) define Angistorhininae by numerous primitive features, but also the arching parieto-squamosal complex (here character 34), however, they focus explicitly on the plesiomorphic state of the parieto-squamosal bar among Phytosauridae as a decisive character (p. 1).

Diagnostic (synapomorphic) characters:

This study identifies Angistorhininae as a well-supported clade of basal Phytosauridae. Two derived characters that are unique among Phytosauria:

character (21): the length of the cojoined parts of the parietals is long, being longer than half the length the frontals. Among the taxa under study, this is only paralleled in the outgroup *Proterochampsa*.

character (34): the parieto-squamosal bar is conspicuously arched rather than essentially straight, a character identified by LONG & MURRY (1995).

Furthermore, the following characters that are homoplastic within Phytosauria are identified as diagnostic for Angistorhininae:

character (24): the parietals form a horizontal ledge overhanging the supraoccipital shelf. In contrast to the principally similar condition uniting *Mystriosuchus*, *Pseudopalatus*, and *Arribasuchus*, the presence of a ledge is not coupled with a rounded shape of the squamosal processes of the parietals nor a narrow parietal-supraoccipital complex, and the ledge thus is much wider.

character (37): reversal to the supraoccipital being predominantly vertical, paralleled in "*Parasuchus hislopi*", *Paleorhinus bransoni*, and *Mystriosuchus*.

Clade J: Unnamed clade

Synonym: BALLEW (1989): unnamed clade, figure 1, node E.

Definition: *Leptosuchus crosbiensis*, *Leptosuchus adamanensis*, *Smilosuchus gregorii*, *Rutiodon carolinensis*, and *Mystriosuchus planirostris*, and all descendants of their closest common ancestor.

Referred genera: *Leptosuchus* CASE, 1922, *Smilosuchus* LONG et MURRY, 1995, *Rutiodon* EMMONS, 1856, *Nicrosaurus* O. FRAAS, 1866, *Arribasuchus* LONG et MURRY, 1995, *Pseudopalatus* MEHL, 1928, and *Mystriosuchus* E. FRAAS, 1896, as defined in subsection 5.2.1.

Diagnostic (synapomorphic) characters:

This clade is diagnosed by only one autapomorphy, which is unambiguously distributed:

character (33[2]): the parieto-squamosal bar is depressed below the level of the skull roof for more than 15% of the skull height.

A long standing problem among the non-angistorhinine phytosaurids is the interrelationships of the basal members from North America now referred to the genera *Rutiodon*, *Leptosuchus*, and *Smilosuchus*. This study failed to resolve the topology of all these taxa satisfactorily. Among the 35 MPTs, the configuration illustrated in Figure 5.5 is the most common and is supported by the reweighting process. The separation of the more derived non-angistorhinine phytosaurids from a clade *Leptosuchus crosbiensis* + *Smilosuchus gregorii* (node L) rests on the acquisition of a medial lamella of the squamosal (28[1]), which is retained (partially in a modified form) in the derived group and takes place convergently only among angistorhinine phytosaurs (*Angistorhinus talainti*). However, this configuration represents only one of several similarly parsimonious alternatives. These include a clade (*Leptosuchus adamanensis* + (*Leptosuchus crosbiensis* + *Smilosuchus gregorii*)), *Rutiodon carolinensis* then being either positioned at the base of a more derived ingroup (Fig. 5.6A), or the outgroup of all non-angistorhinine phytosaurids (Fig. 5.6B). This clade is, however, supported only by two homoplastic and thus not fully satisfactory characters among Phytosauridae: character (5[2]), tripartite dentition, and a reversal to character (2[1]), moderate snout length. Another alternative (Fig. 5.6C) is a monophyletic "*Rutiodon*" (sensu BALLEW 1989), corresponding to Rutiodontinae of LONG & MURRY (1995), in the configuration (*Rutiodon carolinensis* (*Leptosuchus adamanensis* (*Leptosuchus crosbiensis*, *Smilosuchus gregorii*))). However, "*Rutiodon*"/Rutiodontinae turned out to be not supported by any shared character, but to be based only on the absence of the

apomorphies that diagnose the just characterised *Leptosuchus/Smilosuchus*-clade and the more derived clade node N (see below), respectively.

Finally, it turned out that all the various combinations of these taxa root in the coding of character (28) in *Leptosuchus adamanensis*. Scoring this species as 0 (medial lamella of the squamosal absent, as suggested in LONG & MURRY 1995), removed all inconsistencies, leaving a clade (*Leptosuchus adamanensis* (*Leptosuchus crosbiensis*, *Smilosuchus gregorii*)), as outgroup of *Rutiodon carolinensis* + node N (Pseudopalatinae) as in Figure 5.6A. However, I maintain the original coding 1, as long as the primary data of *Leptosuchus adamanensis* as illustrated in CAMP (1930: pl. 1) is not convincingly falsified.

I think it is more significant that the sistergroup *Leptosuchus crosbiensis* + *Smilosuchus gregorii* (node K) is present in all but one of the 35 MPTs. The close relation is well supported by character (29), vertical part of the squamosal enlarged, which is only paralleled in not closely related forms (*Angistorhinus grandis*, *Angistorhinus talainti*, some specimens of *Mystriosuchus planirostris*). Further indications of a sistergroup relationship are character (7), anterior part of septomaxilla elongated, and character (47[2]), suborbital opening reduced to an oval foramen (trait 2a, Tab. B.7), both of which occur convergently among more derived phytosaurids. Cladograms that include a clade *Leptosuchus crosbiensis* and *Leptosuchus adamanensis* are two steps longer than the configurations described above (Tab. 5.1). A monophyletic genus *Leptosuchus* is diagnosable only by the reversal to a moderately long, slit-shaped interpterygoid vacuity (48[1]), which occurred parallel also in *Rutiodon carolinensis* (48[0]). Both the tree length and the quality of the diagnosing character (in comparison with the clade *Leptosuchus crosbiensis* + *Smilosuchus gregorii*) can be seen as fairly strong evidence that *Leptosuchus* is actually an artificial paraphyletic genus. I also wish to point out that similar differences as in the diagnoses of *Leptosuchus* and *Smilosuchus* (degree of heterodonty and associated skull features, robusticity of the skull, skull height, length of the posterior process: BALLEW 1989, LONG & MURRY 1995) exist between both species within the genus *Nicrosaurus*. A solution to this essentially alpha-taxonomic problem should be based on a thorough review of all species involved.

Clade N: Pseudopalatinae LONG et MURRY, 1995

Synonym: BALLEW (1989): unnamed clade, figure 1, node K.

Definition: *Nicrosaurus kapffi* and *Mystriosuchus planirostris*, and all descendants of their closest common ancestor.

Referred taxa: *Nicrosaurus kapffi* (MEYER, 1860), *Nicrosaurus* species B, *Arribasuchus buceros* (COPE, 1881), *Pseudopalatus pristinus* MEHL, 1928, *Mystriosuchus planirostris* (MEYER, 1863), and *Mystriosuchus* species B, as defined in subsection 5.2.1. Pending further investigation, *Coburgosuchus goeckeli* HELLER, 1954 is also referred to this clade.

Discussion: The original diagnosis of Pseudopalatinae is deficient in not fully applying to the taxa included by LONG & MURRY (*Nicrosaurus*, *Arribasuchus*, and *Pseudopalatus*), but rather characterise *Pseudopalatus* and *Arribasuchus* only: The supratemporal fenestrae of *Nicrosaurus* can hardly be described as being narrow (also BALLEW 1989: character 16b) and are not concealed in dorsal view, and the nares is never elevated above the skull roof. The dorsoventrally shallow posterior process of the squamosal, also suggested by BALLEW (1989: character 12b), is a primitive feature of Phytosauridae. Furthermore, BALLEW's character 35, low jugal, is a plesiomorphic character state and varies between the taxa. The only character suggested in LONG & MURRY (1995) and BALLEW (1989: character 34) of substance is the broad and sculptured parieto-squamosal bar (here 20[2]).

Diagnostic (synapomorphic) characters:

character (20[2]): the postorbito-squamosal bar is broad, the ratio of length to width being lesser than 4. Among the taxa under study, a similarly low ratio is only found in the outgroup *Proterochampsa*, and the primitive phytosaur *Francosuchus*.

character (37[2]): the horizontally deflected part of the supraoccipital shelf is elongated. The character is reversed to (37[1]) in *Mystriosuchus*.

Clade O: Unnamed clade

Synonym: BALLEW (1989): unnamed clade, figure 1, node M "*Pseudopalatus*".

Definition: *Arribasuchus buceros* (in the definition in subsection 5.2.1) and *Mystriosuchus planirostris*, and all descendants of their closest common ancestor.

Referred taxa: *Arribasuchus buceros* (COPE, 1881), *Pseudopalatus pristinus* MEHL, 1928, *Mystriosuchus planirostris* (MEYER, 1863), and *Mystriosuchus* species B, as defined in subsection 5.2.1. Pending further investigation, *Angistorhinopsis ruetimeyeri* (HUENE, 1911) and *Machaeroprosopus validus* (MEHL, 1916) are referred to this clade.

Diagnostic (synapomorphic) characters:

(6[2]), (23), (24[2]), (33[3]), and the less unambiguous (1[2]) and (47[2]), see character description in part 5.4.3.2.

Chapter 6

Conclusions

Section 6.1
Summary of the thesis

Following the development of new phylogenetic hypotheses in recent years, there has been a need to reconsider the taxonomy of the Norian phytosaurs from Europe. For this reason, the majority of the thesis is dedicated to clarifying the taxonomy of the phytosaurs from the Stubensandstein of the southwestern Germany, and a comprehensive anatomical description of the cranial material available has been undertaken. This is required to test, emendate, and substantiate reconstructions of the skull anatomy of previous authors in the light of our current knowledge of phytosaur anatomy. The alpha-taxonomy of the specimens and the definitions of the genera involved is based on firmer ground consisting of shared derived characters, rather than overall similarity. The cranial descriptions also provide a basis for detailed comparisons with the remaining European phytosaurs (*Coburgosuchus*, *Angistorhinopsis*) and the North American, Indian, and North African taxa that should be undertaken in the future. Furthermore, the descriptions suggest a variety of new characters that might prove useful for determining the phylogenetic relationships of phytosaurs. A phylogenetic framework for phytosaurs is proposed that includes more taxa, is based on a more comprehensive data matrix, and introduces new characters or redefines previously suggested character states.

In the Stubensandstein, two genera, *Nicrosaurus* and *Mystriosuchus*, are present with at least four well-represented morphospecies.

The genus *Nicrosaurus* is defined by three derived diagnostic characters: an infranasal recess is present between the external nasal opening and the antorbital fenestra and leads to a laterally convex narial bulb, the palatines meet in the mid-line on the palatal vault, and on the braincase, the foramen nervi hypoglossi (XII) is located in the recess

that houses the foramen jugulare (IX-XI). *Nicrosaurus* comprises two species, the type species *Nicrosaurus kapffi* and specimens usually referred to "*Belodon plieningeri*" (sensu MEYER 1861, 1865b), which are identified here as *Nicrosaurus* species B. *Nicrosaurus* seems to be endemic to the lower and middle Stubensandstein of Southwest Germany, and previous claims that the genus is also present in North America (e.g. *Nicrosaurus buceros*) and India (*Nicrosaurus maleriensis*) are found to be unsubstantiated.

Nicrosaurus kapffi is a medium to large, robustly built phytosaur with a conspicuous prenarial crest. The cranial morphology and the osteology is described in detail, and almost all known specimens are figured. As general characteristics of the genus, *Nicrosaurus kapffi* shows the anterior rim of the naris at or somewhat behind the level of the anterior rim of the antorbital fenestra, a broad postorbito-squamosal bar, a parieto-squamosal bar depressed below the level of the skull roof for a distance of approximately 20 to 25% of the skull height, moderately steeply descending squamosal processes of the parietals that meet in an angle, palatines visible on the palatal vault, and long, slit-like suborbital openings. In contrast to *Nicrosaurus* species B, the posterior process of the squamosal is continuously broad, with a thickened medial rim, and the process terminates in a rounded rim, with a posteromedially facing flat surface and ventrally pointing blunt knob. A peculiarity of at least one specimen is the posttemporal fenestra bound ventrolaterally by a stout process of the squamosal that lies on the paroccipital process. The braincase still remains largely unknown. The morphology of the mandibles is very similar to that of lower jaws described for other robust phytosaurs (CAMP 1930; CASE 1930), and can be distinguished from *Nicrosaurus* species B by a shorter symphysis (40% of the mandible length) and a much wider glenoid facet. *Nicrosaurus kapffi* is defined here by two characters of the prenarial crest: all specimens share a continuous crest almost reaching the tip of the snout, and a straight or even convex crest top.

A study of the variation of cranial characters in *Nicrosaurus kapffi* was carried out. A total of 39 characters were identified that show dimorphically or gradually varying character states, and the complementary character states and their distribution among the specimens were described. The variable characters were then tentatively differentiated into ontogenetic, individual and sexually intraspecific variables.

Although no complete ontogenetic series is present, several transformations take place with increasing age: an increase of the width of the snout and the prenarial crest, an expansion of the maxillary flanges in combination with a medial shift of the maxillary tooth row, and a reduction of the suborbital foramen into several smaller foramina.

Specimens vary individually regarding, among other characters, the length and shape of the septomaxilla, the position of the anterior narial rim relative to the anterior border of the antorbital fenestra, the configuration of the bones around the antorbital fenestra and the orbit, the presence of a parietal foramen, the shape of the expanded lateral part of the paroccipital process of the opisthotic, and the depth of the postchoanal palate.

The most significant intraspecific variation is the width-to-height relationship of the postorbital part of the skull: *Nicrosaurus kapffi* can be subdivided into low-domed, robust and high-domed, more gracile morphs. The height of the skull and the overall robustness of a specimen correlate with numerous character states of the postorbital skull (such as the slope of the cheek, the orientation of the orbits and infratemporal fenestra, and the dimensions of the paroccipital process of the opisthotic), of the prenarial crest (in particular the shape of the crest and the width of the crest top), and of the rostrum (e.g. the width of the snout and the presence of maxillary flanges). All these characters are tentatively identified as sexually dimorphic characters.

Among the skull features found to be intraspecifically variable in *Nicrosaurus kapffi*, there are a number of important characters that are currently employed in the alpha-taxonomy of phytosaurs, and characters that have been suggested as diagnostic for higher categories (from generic to subfamily rank). The most important of these are the shape of the prenarial crest and the width of the crest top, the width of the rostrum, the configuration of the bones surrounding the antorbital opening and the orbit, the orientation of the orbits, the presence or absence of a parietal foramen, the slope of the cheeks, the degree of divergence and slope of the squamosal processes of the parietals, the width-to-height relation of the postorbital part of the skull, the position of the choanae, and the reduction of the supratemporal opening. As a consequence, these characters are not used in this study to define species and genera, and were also largely excluded from the data used in the phylogenetic analysis. The intraspecific variation among specimens of the well-defined *Nicrosaurus kapffi* suggests that these characters are probably unsuitable for taxonomic purposes in phytosaurs in general. The variation in phytosaur taxa which have been defined by such characters needs to be determined in order to reestablish the validity of such taxa and emend the diagnoses when necessary.

The dentition of *Nicrosaurus kapffi* is arranged in distinct arrays of teeth, here introduced as dental sets. A dental set is defined by the morphological changes of the teeth occurring within a set. Each dental set occupies a distinct position within the jaws, which in the upper jaw of *Nicrosaurus kapffi* corresponds to the tip of the snout, the post-tip section of the premaxilla, and the maxilla. Consequently, the dentition of *Nicrosaurus kapffi* is defined here as tripartite. For the first time, the positional variation

of the dentition of a heterodont phytosaur, as represented by *Nicrosaurus kapffi*, is described in detail and the tooth types in the dentition are illustrated.
Tripartite dentitions in phytosaurs are contrasted, for instance, by *Nicrosaurus* species B and *Mystriosuchus planirostris*, which show a bipartite upper dentition consisting of a tip-of-snout set and a post-tip set that includes all remaining teeth. Bipartite dentitions lack the straight, large, bicarinate and in cross-section D-shaped teeth occurring in the posterior premaxilla of tripartite forms. In the mandibles of all phytosaur taxa, only a tip-of-mandible and a dentary set are present. The number of dental sets in the upper jaw of phytosaurs, i.e. a tripartite versus a bipartite upper dentition, and the degree of transformation of dental characters applying to a particular set, could be used to define the degree of heterodonty in phytosaurs more objectively than currently practised. Since phytosaur teeth from the anterior positions in the premaxilla, maxilla, and dentary sets largely correspond with a generalised archosaurian tooth type, only teeth from intermediate and posterior positions of these sets can be referred to a particular location in the jaw when found in isolation.

Furthermore, only such teeth have the potential to present taxonomically significant information. Our knowledge of the range of both positional and ontogenetic variation in dental characters of taxa other than *Nicrosaurus kapffi* is still far from sufficient. The taxonomic value of comparisons with other phytosaurs are limited at present. One conclusion is that specimens with bipartite and tripartite dentitions are thus unlikely to belong to the same morphospecies. Some dental characters of other tripartite phytosaur species that differ from those of *Nicrosaurus kapffi* are pointed out. These character states might prove unique for the taxa in question, pending a more comprehensive investigation. Such characters include, for example, the cross-section of the enlarged anterior premaxillary teeth, the ornamentation of teeth, the rates of tooth height increase along the various dental sets, and the position of dental sets relative to the jaw bones. It is nevertheless not advisable as yet to establish phytosaur taxa on isolated teeth. However, it is concluded that a number of dental characters can contribute valuable information to distinguish even closely related phytosaur taxa such as *Nicrosaurus kapffi* and *Nicrosaurus* species B.

Nicrosaurus species B includes the specimens usually referred to "*Belodon plieningeri*" (sensu MEYER 1861 and 1865b). These are moderate-sized, gracile, and slender-snouted phytosaurs. Many of the following characteristics and distinguishing characters from *Nicrosaurus kapffi* are derived from skull SMNS 12593, the only complete specimen known, which is described for the first time.

In *Nicrosaurus* species B, a narial wing is frequently present and the posterior part of the naso-septomaxillary suture forms a deep groove in front of the nares. The sculpture of the preorbital region is much more prominent. There is always a well developed longitudinal depression in the cheek region. In the temporal region, the dorsal rim of the squamosal process of the parietals slopes more gently and is posteromedially deflected over the supraoccipital shelf leading to an occipitally facing groove. The length of the squamosal body is increased resulting in a wider tympanic fossa. In dorsal view, the posterior process of the squamosal is continuously broad, and the medial rim is angular and not significantly thickened. The posterior process of the squamosal terminates in a pointed tip. In the braincase, the opisthotic lamella between the stapedial and the jugular groove is low, blunt, and thick. The upper jaw dentition is bipartite, i.e. it contains only two sets of teeth.

Nicrosaurus species B is compared in detail with *Nicrosaurus kapffi* and the more derived *Pseudopalatus pristinus*. Although some specimens show several characters more derived than in *Nicrosaurus kapffi* (e.g.: raised narial rims, an elongated squamosal body, an angular squamosal with a pointed tip and an apparently reduced width of the supratemporal fenestra), there are a variety of problems with these characters. The character states are poorly defined, their distribution within phytosaurs is uninformative or unknown, and, most importantly, because of the incompleteness of most specimens it is unclear whether they are representative for the taxon *Nicrosaurus* species B or indicate intraspecific variation. *Nicrosaurus* species B is conservatively defined by only one shared derived character: the parieto-squamosal bar is low, showing a maximum thickness of about 10 mm.

As in *Nicrosaurus kapffi*, *Nicrosaurus* species B includes a high-domed and a low-domed morph. However, in the high-domed specimens, the skull is absolutely higher and these specimens are not particularly gracile compared to the low-domed morph. Moreover, the specimens vary between being crest-less and having a partial, sharp prenarial crest, and in the absence or presence of a narial wing. The presence of these character states is not correlated with skull height.

A reinvestigation of *Mystriosuchus* was necessary because the identification of a new, still unnamed species (HUNT & LUCAS 1989b; LONG & MURRY 1995; here *Mystriosuchus* species B) leaves some previously defined diagnostic characters of the genus as diagnostic for the type species *Mystriosuchus planirostris* only, or necessitates a redefinition of other characters. Furthermore, the diagnostic nature of several significant characters depends on the debated position of the genus within a phylogenetic framework of phytosaurs.

The genus *Mystriosuchus* is redefined by a total of nine diagnostic characters: an elongated rostrum, the interpremaxillary fossa is reduced to a slit, a particular and deep sculpture of the skull roof and the narial region, a preorbital depression, an anteroposteriorly wide pre-infratemporal shelf, a raised anterior border of the supratemporal fenestra, a dorsoventrally thick parieto-squamosal bar with a triangular cross-section, the extremely reduced posttemporal fenestra, and a vertically descending squamosal process of the parietal. In Germany, *Mystriosuchus* is restricted to the middle Stubensandstein, but *Mystriosuchus planirostris* occurs also in the Middle Norian of Austria and Italy.

Mystriosuchus is a highly derived clade of two medium to large-sized morphospecies with slender and elongated snout. *Mystriosuchus planirostris* may be used to characterise the skull morphology of the genus. The anterior rims of the crater-like nares are at the level of the anterior rim of the antorbital fenestrae, and a large narial wing is always present. The postorbital part of the skull is narrow, high, and anteroposteriorly abbreviated. The supratemporal fenestra is fully open dorsally, and the posterior process of the squamosal is very short or not developed. The parieto-squamosal bar is greatly depressed below the level of the skull roof by at least 25% of the skull height, and closely appressed on the paroccipital process of the opisthotic. This results in a high, narrow supraoccipital shelf. The dentition of both species is probably bipartite.

Mystriosuchus planirostris, the type-species of the genus, is redefined. The rostrum is longer, and the prenarial region slopes steeply down immediately in front of the naris. The naris is separated into a dorsal and an anteriorly facing part with a protruding internasal septum bearing perpendicular dorsal and anterior rims. The depression of the parieto-squamosal bar reaches its maximum among phytosaurs, exceeding 30% of the skull height, and the posterolateral borders of the supratemporal fenestra are raised. The teeth of *Mystriosuchus planirostris* are slender, basally fluted, and show one weak distal carina at best, but small bicarinate teeth occur in the posteriormost part of the maxilla. The symphysis of this species is long, reaching 60% of the total length of the mandible.

A large skull (GPIT 261/001) and a snout fragment (GPIT 261/17/7) are redescribed and previous interpretations of the specimen as an new species (*Mystriosuchus* species B) are substantiated. *Mystriosuchus* species B is diagnosed by prominent anterior sections of the alveolar ridges, the parietal process of the squamosal participates in the rim of the supraoccipital shelf, a lamina of the parietal process of the squamosal contacts the prootic, a lobate extension on the vertical rim of the squamosal processes of the parietal, and the posttemporal fenestra is reduced to a narrow slit. The

new species is also distinguished from the type species, *Mystriosuchus planirostris*, by numerous characters, among them larger size, a shorter and more robust rostrum, a gently sloping snout profile, probably a higher degree of heterodonty, and a squamosal that has a blunt extremity and lacks a posterior process. In both specimens, a short crest on the premaxilla demonstrated for the first time in a phytosaur taxon is present. Teeth and lower jaws are unknown in *Mystriosuchus* species B.

GPIT 261/001 shows a paired orbitosphenoid in the anterior part of the neurocranium and corroborates similar findings of CAMP (1942) in *Smilosuchus gregorii*. An additional ossification is present in the occipital region, separating the parietal from the squamosal on the rim of the supraoccipital shelf. This bone, identified as a tabular by CAMP (1930) in *Smilosuchus*, more likely represents a neomorphic ossification. This neomorphic bone is homologised with a lamina of the squamosal process of the parietal that descends onto the supraoccipital shelf in other phytosaurs, and it is concluded that the bone may be retained as a discrete element in some individuals. There is no evidence in GPIT 261/001 for a discrete presphenoid as described in "*Parasuchus*" and *Smilosuchus* (CHATTERJEE 1978; CAMP 1930, 1942).

Belodon plieningeri, based on a tooth and a mandibular fragment with a posterior dentary tooth, is indeterminable beyond Phytosauria and the taxon is thus a *nomen dubium*. However, the teeth are not identical to those of *Nicrosaurus* species B, the "*Belodon plieningeri*" of numerous previous authors, but belong to a phytosaur with a more robust dentition. Similarly, *Phytosaurus cylindricodon* and its junior synonym *Phytosaurus cubicodon*, the type genus of Phytosauridae, is identified as the mould of a mandible of an indeterminate, but strongly heterodont phytosaur.

Phytosauria is characterised by numerous autapomorphies, many of them related to the semiaquatic habit of these animals, and is thus one of the best established natural groups among archosaurs. A phylogenetic analysis of almost all named phytosaur species (in the cases of taxa not present in the Stubensandstein regardless of their validity) was undertaken, using a total of 49 characters. Only three clades of suprageneric rank within Phytosauria are found to be robust: these are (1) Phytosauridae (sensu DOYLE & SUES 1995), which consists of the subclades (2) Angistorhininae (*Brachysuchus megalodon*, *Angistorhinus grandis*, and *Angistorhinus talainti*) and (3) a clade comprising all other phytosaurids. The postulated clade Paleorhininae (LONG & MURRY 1995, identified as an unnamed monophylum by BALLEW 1989), which comprises all the primitive genera *Arganarhinus*, *Ebrachosuchus*, *Francosuchus*, *Mesorhinosuchus*, "*Parasuchus*", *Paleorhinus*, and *Promystriosuchus*, is found to be very weakly supported. The

subfamily Paleorhininae most likely represents a paraphyletic assemblage of the most primitive phytosaurs known. Consequently, the assemblage is addressed here as non-phytosaurid phytosaurs, an assemblage of genera that form the stem-group of Phytosauridae. It is demonstrated that *Mystriosuchus* is not the sistergroup of "Paleorhininae", nor of any single taxon among primitive phytosaurs, but a highly derived phytosaur nested deeply within Phytosauridae (contra HUNT 1994 and LONG & MURRY 1995). This suggests that the characteristic backward-shift of the nares to a position in front of the orbits and the depression of the parieto-squamosal bar took place only once among phytosaurs, and represent synapomorphies of Phytosauridae, and a clade consisting of all Phytosauridae except Angistorhininae, respectively. Furthermore, in *Mystriosuchus* the posterior process of the squamosal is secondarily greatly reduced or entirely lost, the supratemporal fenestra has reverted to a fully dorsally open condition, and the genus acquired its long snout independently from *Ebrachosuchus*.

Section 6.2
Prospectus

Although *Nicrosaurus kapffi* is well known, more data of the braincase is urgently required and the configuration of the bones around the posttemporal fenestra and in the occipital region, suggested here, should be confirmed by repreparation of the existing specimens. Non-invasive techniques such as CT scans might prove useful for investigating the pneumatisation of the prenarial crest and the snout. *Nicrosaurus* species B is still incompletely known. However, new finds are needed for data on the dentition, and to corroborate the structure of the temporal and occipital regions of SMNS 12593 and put the conclusions regarding the prenarial crests to the test.

Although both species are defined by shared derived characters, the specific segregation of *Nicrosaurus*, and the sexual dimorphism suggested at species level here might be further tested by scoring the variable character states for each specimen, and processing these data using multivariate statistics or PAUP.

The numerous specimens of *Mystriosuchus planirostris* offer an opportunity to determine the variation of cranial character states in a second phytosaur species. The genus is currently regarded as a taxon that shows less variable cranial characters (HUNT & LUCAS 1989b), but the temporal region of *Mystriosuchus planirostris* (subsection

2.2.3) and the redescription of *Mystriosuchus* species B (subsection 2.2.3) suggests otherwise. The data should then be compared with the variation seen in *Nicrosaurus kapffi*, in order to obtain information about the amount of variation of the same character in two genera, and about the general taxonomic and phylogenetic relevance of the conclusions drawn in subsection 2.2.7. Secondly, there is the potential to corroborate the nature and significance of the braincase characters described in *Mystriosuchus* species B (orbitosphenoid, presphenoid, additional occipital bone). However, this would require intensive repreparation of the specimens, and the Austrian and Italian finds should also be considered.

Another important conclusion of this work is that the alpha-taxonomy of phytosaurs is a much more complex and difficult issue than it appears from the literature, and the current diagnoses of numerous taxa are probably oversimplified. This is particularly the case in the specimens currently referred to the genera *Paleorhinus* and *Arganarhinus* (BALLEW 1989; HUNT & LUCAS 1991; LONG & MURRY 1995), which are both in need of revision at species level. A sound taxonomy of primitive phytosaurs is urgently needed as a basis for an analysis of the ingroup relationships of phytosaurs. It is also important to note that the genus *Leptosuchus*, which has been tentatively suggested to include *Leptosuchus crosbiensis* and *Leptosuchus adamanensis*, and might even be considered conspecific (LONG & MURRY 1995: 43), consistently turned out to be paraphyletic, and in a number of trees, the two species are placed far away from each other in different subclades. This means that *Leptosuchus* is either very poorly diagnosed or indeed is not a natural group. There is also no evidence for a clade Rutiodontinae (*Rutiodon* + *Leptosuchus* + *Smilosuchus*), despite their alleged very close similarity (BALLEW 1989; LONG & MURRY 1995). Some serious deficiencies in the diagnoses of *Pseudopalatus* and *Arribasuchus* (e.g. the elevation of the nares, crater-like nares, and the closure of the supratemporal opening) were also pointed out.

The phylogenetic hypothesis presented here is still a preliminary one. The analysis revealed that the ingroup relationships within the clade Phytosauridae (Angistorhininae + *Leptosuchus* + *Smilosuchus* + *Rutiodon* + *Nicrosaurus* + *Arribasuchus* + *Pseudopalatus* + *Mystriosuchus*) on the basis of the data matrix presented in Appendix A is not particularly robust. This is in parts a consequence of the incomplete knowledge of the actual morphology, and the distribution among these taxa, of numerous character states used in the phylogenetic analysis. Furthermore, a number of characters suggested for the first time in this study are still in need of substantiation. However, there is also a prospective field for future research in obtaining new data, in particular regarding

characters of the braincase and the palate, skull regions which have been generally poorly described in phytosaurs, but seem to have the potential of providing significant new phylogenetic information.

Chapter 7

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